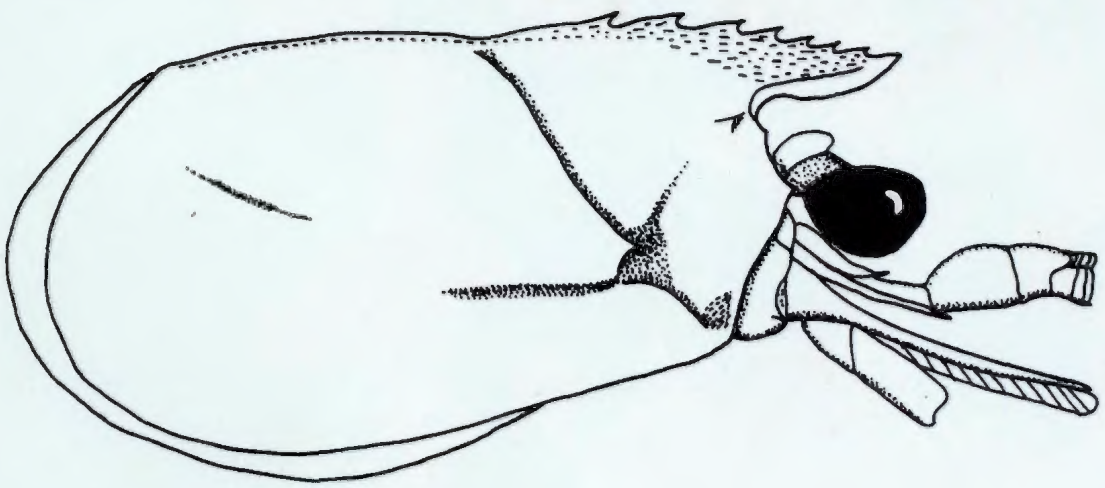
# MEMOIRS

OF THE

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BRISBANE
30 JUNE 1999

VOLUME 43
PART 2

# THREE NEW SPECIES OF MELOLONTHINI (COLEOPTERA: SCARABAEIDAE) FROM AUSTRALIA

P.G. ALLSOPP

Allsopp, P.G. 1999 06 30: Three new species of Melolonthini (Coleoptera: Scarabaeidae) from Australia. *Memoirs of the Queensland Museum* **43**(2): 453-458. Brisbane. ISSN 0079-8835.

Three new species are described from Australia: *Lepidiota bakkeri* sp. nov. from Broome, Western Australia, *L. clareae* sp. nov. from Hopevale, NE Queensland, and *Metatrogus lukei* sp. nov. from Sunshine Beach, SE Queensland. The three species are illustrated and compared with known species. Some specimens previously attributed to *L. negatoria* Blackburn are identified as *L. frenchi* Blackburn. ❐ *Coleoptera, Scarabaeidae, Melolonthinae, Lepidiota, Metatrogus, taxonomy.*

*P.G. Allsopp, Bureau of Sugar Experiment Stations, PO Box 651, Bundaberg 4670, Australia; 8 December 1998.*

The Australian Melolonthini were last revised by Britton (1978) and the tribe in Australia is now known to contain 16 genera and 116 species (Houston & Weir, 1992; Allsopp, 1993a,b,c; Allsopp & Watkins, 1995). Most of the species occur in the N and E of the continent, with *Lepidiota* Kirby and *Dermolepida* Arrow extending into SE Asia and New Guinea, respectively (Allsopp, 1995).

This paper describes 3 new species; 2 from E Queensland, and 1 from NW Western Australia. Abbreviations: ANIC, Australian National Insect Collection, Canberra; AWA, Agriculture Western Australia, Perth; PA, P. Allsopp collection; PB, Peter Bakker collection; QM, Queensland Museum, Brisbane; QPIM, Queensland Department of Primary Industries, Mareeba; WAM, Western Australia Museum, Perth.

## **Lepidiota** Kirby

*Lepidiota* Kirby, 1828: 445.

TYPE SPECIES: *Melolontha stigma* Fabricius, subsequent designation by Hope (1837).

DIAGNOSIS. Britton (1978) distinguished *Lepidiota* from other Australian Melolonthini by a combination of: anterior face of clypeus shallow and usually smooth and unpunctured in the middle; anterior edge of clypeus as seen from above usually broadly bilobed; antennae 10- (rarely 9-) segmented, with a 3-segmented club; lamellae usually shorter than antennal segments 1-7 (or 1-6) together; surface of the body usually bearing few or many broad, adpressed, white scales, scales sometimes minute and wholly contained within their punctures; tarsal claws each with a strong tooth in the middle of the concave side; anterior edge of posterior femora not concave near the base; mandibles not curved downwards at their apices.

Sixty species are known to occur in Australia, mainly in the north half of the continent (Britton, 1978; Houston & Weir, 1992; Allsopp & Watkins, 1995).

### **Lepidiota bakkeri** sp. nov.
(Fig. 1)

ETYMOLOGY. For my colleague Peter Bakker, Bureau of Sugar Experiment Stations, who collected the type series.

MATERIAL. HOLOTYPE: QMT62716, M, Broome (Western Australia), 27.x.1996, P. Bakker, at lights. PARATYPES: 10M, F, same data as holotype (ANIC, AWA, PA, QM, WAM).

DESCRIPTION. *Male*. Body 23-25mm long. Head, pronotum, pygidium, venter and legs reddish brown, elytra paler and with a dull sheen; antennae yellow-brown to dark brown. Labrum deeply indented, about twice as deep as the anterior face of the clypeus, each lobe with a few scattered, setose punctures, middle section glabrous. Labrum not visible beyond the clypeus in front. Clypeus with anterior face shallow, 7-8x as wide as deep, with a single row of setiferous punctures interrupted in the middle; upper surface almost straight in outline, transverse, 3x as wide as long, covered with almost circular, white scales, except for a bare area in the middle. Anterior 2/3 of the frons with similar scales; posterior surface with a very dense band of

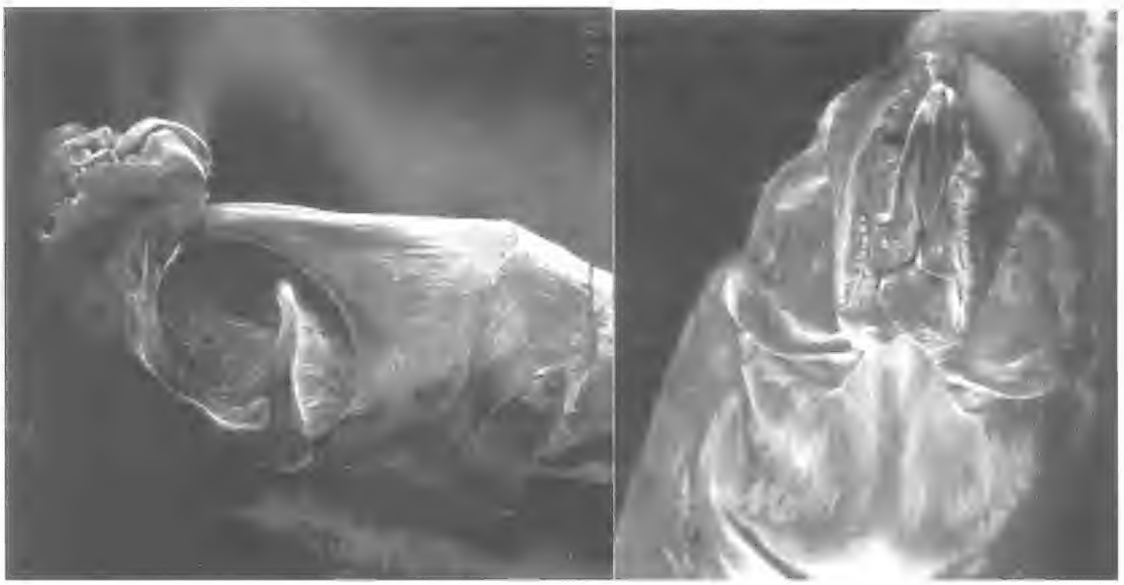


FIG. 1. *Lepidiota bakkeri*, male parameres.

smaller, more elongate scales with a small bare area in the middle. Antennae 10-segmented, club 3-lamellate, club 1.3mm long and as long as segments 2-7 combined. Pronotum with greatest width 1.6 times the mid length, lateral edges obviously angulate in middle, edges behind these angles almost parallel when seen from above; anterior and posterior angles slightly obtuse; without defined anterior and posterior margins; surface densely clothed with scales except for a bare area along the midlongitudinal line which is wider on the posterior half than on the anterior half. Scutellum with elongate scales, except on the midlongitudinal line. Elytra densely and uniformly clothed with white scales, except on the humeri where the scales are sparser. Propygidium with a uniform and very dense clothing of small, ovate, whitish scales on the posterior three-quarters, merging into recumbent setae anteriorly. Pygidium densely clothed with oval, white scales. Pronotal hypomera, metepisternum, metasternum and hind coxae with white scales and a few long, thin, yellow setae, setae denser and scales sparser towards the middle of the metasternum. Abdominal sternites with dense, white scales, scales sparser on the last segment. Parameres almost symmetrical, with a prominent basal process (Fig. 1).

*Female.* Body 24mm long. Similar to male, except antennal club 1.2mm long, shorter than segments 2-7 combined.

COMMENTS. *L. bakkeri* is very similar to *L. delicatula* Blackburn and *L. arnhemensis* Britton and keys to couplet 44 in Britton's (1978) key to Australian *Lepidiota*. It can be distinguished from those species only by the shape of the aedeagus (compare Fig. 1 with Britton's (1978) figs 247-250); the shape of the basal process distinguishes *L. bakkeri* from *L. arnhemensis*.

**Lepidiota clareae** sp. nov.
(Fig. 2)

ETYMOLOGY. For my daughter Clare Allsopp.

MATERIAL. HOLOTYPE: ANIC122, M, 14km WbyN Hope Vale Mission (Hopevale, Qld) 15.16°S, 144.59°E, 7-10.v.1981, A. Calder, at light. PARATYPE: F, same data as holotype (ANIC).

DESCRIPION. *Male.* Body 23.5mm long. Head, pronotum and ventral thorax dark reddish brown, elytra and abdomen lighter reddish brown, dorsal and ventral surface with white scales, antennae dark brown. Labrum deeply indented, about 5x as deep as the anterior face of the clypeus, each lobe and middle section with scattered, setose punctures. Labrum just visible beyond the clypeus in front. Clypeus with anterior face very shallow, about 11x as wide as deep, with scattered setiferous punctures laterally, interrupted in the middle by bare area; upper surface indented in middle transverse, about 4x as wide as long, covered with scattered, almost

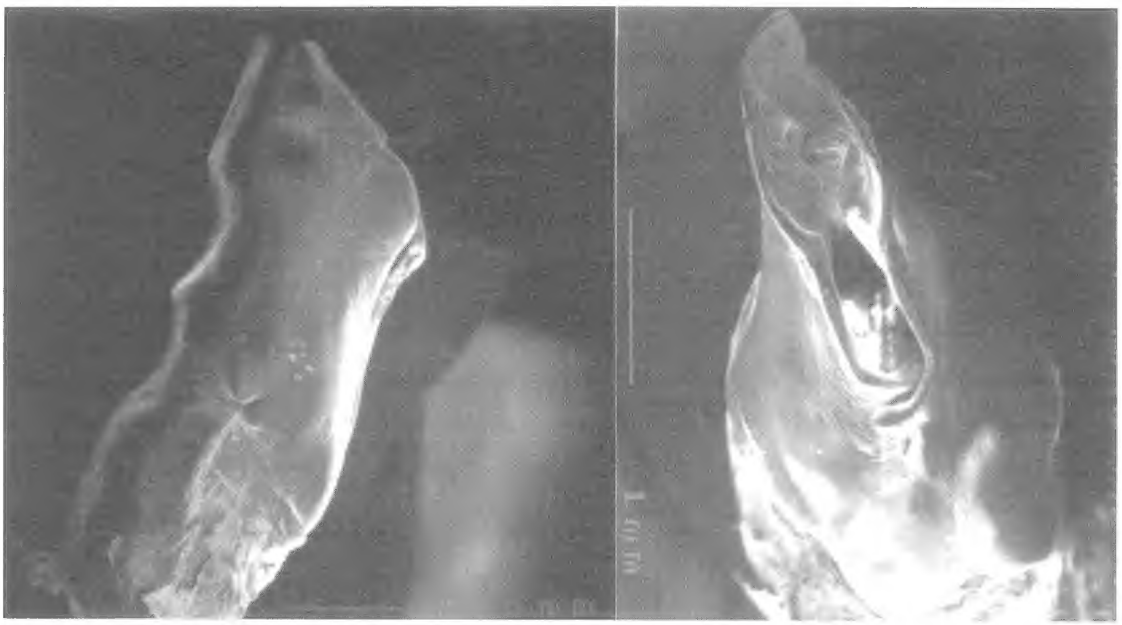


FIG. 2. *Lepidiota clareae*, male parameres.

circular, white scales, except for bare triangular area in the middle along the posterior margin. Frons with anterior part evenly punctate, each puncture bearing a white scale, punctures and scales more dense above the eyes; posterior third with a dense band of elongate scales and then bare posteriorly. Antennae 10- segmented, club 3-lamellate, club 1.3mm long and as long as segments 2-7 combined. Pronotum slightly wider across base than in middle, greatest width 1.7x the mid length, lateral edges obviously angulate in middle, edges behind these angles almost parallel when seen from above but each indented slightly; anterior angles obviously obtuse, posterior angles square; with defined anterior and posterior margins; surface densely clothed with rounded scales, scales more densely crowded towards the posterior part of the lateral margins and especially on the posterior margin. Scutellum with circular scales smaller and denser across anterior quarter, larger and more scattered on remainder. Elytra uniformly clothed with white, circular scales. Propygidium without a ridge above each posterior angle on each side, scales on posterior third small, circular to slightly elongate, fairly uniform in size and separated by 1 diameter or more. Pygidium densely clothed with oval, white scales, scales denser and more elongate medially and towards apex. Pronotal hypomera with elongate scales except in a median transverse band. Metepisternum, mesepisternum and metepisternum with elongate scales. Metasternum clothed with long, fine, yellowish setae except for elongate scales across the median base and in the posterior lateral angles. Hind coxae with elongate, white scales on outer two-thirds, inner third with long, fine, yellowish setae. Abdomen with sternites 2-4 densely clothed with circular, white scales at the sides, becoming sparser in the middle of each sternite and absent from the middle of the anterior margins of sternites 3 and 4; sternite 5 with scales more evenly distributed across surface. Parameres almost symmetrical, without prominent processes (Fig. 2).

*Female.* Body 26mm long. Similar to male, except antennal club 1.2mm long, shorter than segments 2-7 combined, apex of pygidium more rounded and almost bare of scales.

COMMENTS. *L. clareae* is similar to *L. negatoria* Blackburn and keys to that species in Britton's (1978) key. The type series was originally placed under *L. negatoria* in the ANIC. *L. clareae* has much denser scales on the pygidium, these scales are circular laterally but become more elongate medially and towards the apex; in *L. negatoria* the pygidium has sparse, circular scales. The two species also differ in the shape of the parameres (compare Fig. 2 with Britton (1978) figs 166-167).

### **Lepidiota frenchi** Blackburn

*Lepidiota frenchi* Blackburn, 1912: 64; Britton, 1978: 58.

MATERIAL. 2F, Mt Spec (Qld), i.1968, E.E. Adams; M, F, 4km W of Running River W of Paluma, 11.i.1987, E.E. Adams; F, The Saddle, Paluma Rd, Mt Spec Nat. Pk, 1.xii.1968, Britton & Misko (all ANIC).

COMMENTS. All of the above specimens were placed as *L. negatoria* in the ANIC; the first two were also placed as that species by Britton (1978). All are *L. frenchi*; this is confirmed by dissection of the parameres of the Y. *L. negatoria* is not known north of Proserpine, about 300km southeast of Mt Spec.

### **Metatrogus** Britton

*Metatrogus* Britton, 1978: 28.

TYPE SPECIES: *Metatrogus septuosus* Britton, by original designation.

DIAGNOSIS. Britton (1978) distinguished *Metatrogus* from other Australian Melolonthini by a combination of: body reddish brown, very dark brown or black with a greyish, pruinose film; anterior face of the clypeus broad and shallow (greatest width: mid length about 8:1), bearing a single, transverse row of setiferous punctures; anterior edge of the clypeus as seen from above uniformly convex, not emarginate or bilobed; antennae 10-segmented with a 3-, 6- or 7-lamellate club; head, pronotum and elytra sparsely punctured, the punctures bearing minute setae, the body without scales, but with flattened, adpressed, white setae on the pronotal hypomera and the abdominal ventrites, pygidium and propygidium; pronotum with or without a narrow, defined anterior margin near the angles only, without a defined posterior margin; scutellum densely punctured; sutures separating ventrites 3-5 fainter in the middle than at the sides; claws with a prominent tooth in the middle of the concave side.

Three species have been described previously (Britton, 1978; Houston & Weir, 1992): *M. septuosus* Britton from SE Queensland and NE New South Wales; *M. praeceps* Britton from the Paluma area, NE Queensland; and *M. castaneus* Britton from Stanthorpe, SE Queensland.

### KEY TO MALES OF *METATROGUS*

1. Antennae with a 3-lamellate club; body very dark brown; parameres as in Britton (1978, figs 77-79) . . . . . *M. praeceps* Britton

   Antennae with a 6-lamellate club; body bright reddish brown; parameres as in Britton (1978, figs 80-82) . . . . . *M. castaneus* Britton

   Antennae with a 7-lamellate club; head and pronotum black, elytra and abdomen dark reddish brown, dorsum with a dull pruinose bloom . . . . . 2

2. Lamellae of antennal segments 6-10 3.3mm long, lamella of segment 4.75 as long as those of segments 6-10; setae of pronotum minute, about as long as the diamter of their punctures; parameres slightly asymmetrical (Britton, 1978, figs 74-76) . . . . *M. septuosus* Britton

   Lamellae of antennal segments 6-10 2.4mm long, lamella of segment 4.5 as long as those of segments 6-10; setae of pronotum 3-4x as long as the diameter of their punctures; parameres symmetrical (Fig. 3) . . . . *M. lukei* sp. nov.

### **Metatrogus lukei** sp. nov.
### (Fig. 3)

ETYMOLOGY. For my son Luke Allsopp, who collected the first 2 specimens.

MATERIAL. HOLOTYPE: QMT62717, Y, Sunshine Beach (Qld), 28.ix.1996, L. Allsopp. PARATYPES: 1X, same data as holotype (ANIC); 2M, 2F, 2 (sex unknown, damaged), same locality, 15.xii.1996, 10.i.1999, P. Allsopp; 3F, same locality, 26-29.ix.1997, P. & L. Allsopp; F, Little Cove, Noosa Heads, 9.i.1999, P. Allsop; F, same locality, 10.i.1999, R. Lloyd (ANIC, PA, QM, QPIM).

DESCRIPTION. *Male.* Body 27-28mm long. Head and pronotum black with a pruinose bloom; elytra dark brown to black with a pruinose bloom; pygidium dark brown; venter and legs dark brown to black; antennae yellow-brown to dark brown. Labrum indented, 1.8x deeper than anterior face of the clypeus, surface with a few scattered, setose punctures. Labrum visible beyond the clypeus in front. Clypeus with anterior face shallow, 8.5x as wide as deep, with a single row of setiferous punctures not interrupted in the middle; upper surface slightly convex in outline, transverse, 3.6-4x as wide as long, coarsely punctured, punctures with stout, pointed, yellowish setae which project beyond their punctures. Anterior 2/3 of the frons similarly punctured, except setae above the eyes denser and 2-3x longer; posterior surface with very few setae in the middle and finer setae towards the edges. Antennae 10-segmented, club 7-lamellate, lamellae of segments 6-10 2.4mm long, segment 5 1.8-2mm long, segment 4 1.3mm long. Pronotum with greatest width 1.6x the mid length, width at base 1.7x width at apex, anterior and posterior angles slightly obtuse, posterior angles slightly rounded, without raised anterior or posterior margins; surface finely punctured, each puncture with a yellowish, flattened, pointed seta 3-4x as long as




FIG. 3. *Metatrogus lukei*, male parameres.

the diameter of the puncture, punctures denser towards the margins, midlongitudinal line unpunctured except for the posterior fifth. Scutellum with similar setose punctures, less dense on the mid-longitudinal line. Elytra uniformly punctured, most punctures with a seta similar to those on the pronotum. Propygidium with anterior 3/4 smooth and glabrous, posterior quarter with flattened, pointed, yellowish setae, setae shorter than on the elytra. Pygidium with the surface rugulose, densely clothed with setae similar to those on the propygidium, except in a bare, longitudinal area in the middle. Pronotal hypomera with long, flattened, whitish setae with a few long, thin, yellow setae. Metasternum, mesosternum and hind coxae clothed densely with long, fine yellowish setae. Abdominal sternites with dense, flattened, adpressed, white setae, setae absent from anterior and posterior edges across the middle, sutures fainter in the middle than at the sides. Femora and tibiae with flattened, adpressed, white setae as well as pointed, yellow setae; claws with a prominent tooth in the middle of the concave side. Parameres symmetrical, rounded across the apices (Fig. 3).

*Female.* Body 29-30mm long. Similar to male, except antennal club 6-lamellate, segments 7-10 1.2mm long, segment 6 1.1mm long, segment 5 0.8mm long.

COMMENTS. The type series was collected at light or in spiders' webs at 2 sites where the soil is very sandy ('Wallum' country). *M. lukei* differs from *M. castaneus* and *M. praeceps* by having 7-lamellate antennal clubs and the head and pronotum black and elytra dark reddish brown, all with a dull pruinose bloom. It is most closely related to *M. septuosus* but has smaller antennal lamellae, longer setae on the pronotum and symmetrical parameres (compare Fig. 3 with Britton, 1978, figs 74-76). *M. septuosus* occurs in areas to the south and west, usually away from the coast, and apparently in areas with soils of higher clay contents.

## ACKNOWLEDGEMENTS

I thank Peter Bakker and Tom Weir (ANIC) for the gift and loan, respectively, of specimens.

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# HOST RANGE OF *PARATHELANDROS MASTIGURUS* (NEMATODA: OXYURIDA) IN AUSTRALIAN AMPHIBIANS

DIANE P. BARTON

Barton, D.P. 1999 06 30: Host range of *Parathelandros mastigurus* (Nematoda: Oxyurida) in Australian amphibians. *Memoirs of the Queensland Museum* **43**(2): 459-461. Brisbane. 0079-8835.

During a survey of the helminth parasites in a total of 24 amphibian species in northern Australia, the nematode *P. mastigurus* was found in 8 of those species collected. Host records include 2 of the 3 species already listed as hosts, and 6 are recorded as new hosts for *P. mastigurus* in Queensland: *Crinia deserticola*, *Limnodynastes tasmaniensis*, *Mixophyes* sp., *Litoria inermis*, *Litoria rothii* and *Litoria rubella*. ❐ *Amphibia, Nematoda, Parathelandros mastigurus, parasites, Australia.*

*Diane P. Barton, School of Tropical Biology, James Cook University, Townsville 4810, Australia; 15 March 1999.*

*Parathelandros mastigurus* (Oxyurida) was described from *Litoria* (=*Hyla*) *caerulea* and *L. gracilenta* in the Townsville region (N Queensland) by Baylis (1930). Since that time, *P. mastigurus* has been reported also to infect the introduced toad *Bufo marinus* in Brisbane, SE Queensland (Inglis, 1968). This Oxyurid genus is known exclusively from amphibians in Australia (Petter & Quentin, 1976) and has not been recorded from *B. marinus* elsewhere in the world. Thus, *P. mastigurus* is a parasite that has been acquired by the introduced toad from native Australian amphibians.

During a survey of the helminth parasites of amphibians in northern Australia, the nematode *P. mastigurus* was found in various amphibian species. Twenty-four amphibian species were collected throughout Queensland and the eastern part of the Northern Territory from 1989 to 1992. Amphibians were collected from the following localities: Abergowrie, Qld, 146°00'E 18°27'S; Bentley, Qld, 146°57'E 19°22'S; Black Rock, Qld, 144°07'E 19°05'S; Bloomfield, Qld, 145°21'E 15°56'S; Boyne Island, Qld, 151°21'E 23°57'S; Brisbane, Qld, 153°01'E 27°30'S; Calvert Hills, NT, 137°25'E 17°13'S; Cape Tribulation, Qld, 145°29'E, 16°05'S; Cape Weymouth, Qld, 143°23'E 12°55'S; Cape York ('Somerset'), Qld, 142°31'E 10°41'S; Charters Towers, Qld, 146°11'E 19°53'S; Coen, Qld, 143°12'E 13°57'S; Mackay, Qld, 149°11'E 21°09'S; Mareeba, Qld, 145°25'E 17°00'S; Mountain View Road, Qld, 146°57'E 19°30'S; Paluma, Qld, 146°12'E 19°01'S; Port Douglas, Qld, 145°28'E, 16°29'S; Townsville, Qld, 146°49'E 19°15'S; Yungaburra, Qld, 145°35'E 17°17'S. Eight of those species (see Table 1), including two of the three species already listed as hosts, were found to be infected with *P. mastigurus*. Thus, six amphibian species are recorded as new hosts for *P. mastigurus* in Queensland: *Crinia deserticola*, *Limnodynastes tasmaniensis*, *Mixophyes* sp., *Litoria inermis*, *Litoria rothii* and *Litoria rubella*.

A major failing in the publication of many plant and animal surveys and in some uses of museum biological data (e.g. modelling the distributions of plant or animal species) is that absence data are not recorded. Similarly, in many parasite surveys uninfected hosts are usually not listed. Thus, the full extent of the survey remains unknown and the data cannot be used in the development of predictive models of the host, and geographic distributions of parasite species. To rectify this situation, the amphibian species investigated in this study that were uninfected and their geographical localities are included (Table 2). Due to the low number of host specimens examined from many localities, this list should not be treated as definitive but used as an aid in determining potential hosts for further examination.

Members of the genus *Parathelandros* are characterised as parasites of the lower alimentary canal of amphibians and are restricted to the Australo-Papuan region (Inglis, 1971; Anderson, 1992). Eight species within the genus *Parathelandros* have been reported, all from frogs; seven of the species have been reported from Australia, the eighth species from a New Guinean microhylid (Moravec 1990). Inglis (1971) suggested that *Parathelandros* was strictly host specific at the level of host genus.

TABLE 1. Amphibian host species infected with *Parathelandros mastigurus*, and their geographical locations in northern Australia.

| Host species | Geographical location | Number of hosts examined | Prevalence | Mean intensity | Maximum infection |
|---|---|---|---|---|---|
| *Crinia deserticola* | Bentley | 8 | 12.5 | 1.0 | 1 |
| *Limnodynastes tasmaniensis* | Townsville | 9 | 11.1 | 3.0 | 3 |
| *Mixophyes* sp. | Mt Lewis | 1 | 100.0 | 28.0 | 28 |
| *Litoria caerulea* | Townsville | 8 | 12.5 | 8.0 | 8 |
| | Abergowrie | 7 | 85.7 | 8.0 | 39 |
| *Litoria inermis* | Townsville | 5 | 60.0 | 7.0 | 10 |
| | Bentley | 141 | 27.0 | 2.7 | 10 |
| | Mountain View Road | 16 | 18.8 | 4.3 | 10 |
| *Litoria rothii* | Townsville | 18 | 22.2 | 8.8 | 24 |
| | Bentley | 2 | 100.0 | 7.0 | 8 |
| | Abergowrie | 1 | 100.0 | 5.0 | 5 |
| *Litoria rubella* | Townsville | 28 | 75.0 | 5.5 | 18 |
| | Bentley | 1 | 100.0 | 1.0 | 1 |
| | Mountain View Road | 5 | 80.0 | 23.3 | 36 |
| *Bufo marinus* | Bentley | 186 | 4.8 | 13.9 | 70 |
| | Mountain View Road | 92 | 3.3 | 3.0 | 5 |
| | Bloomfield | 52 | 5.8 | 2.0 | 12 |
| | Cape Tribulation | 13 | 23.1 | 18.3 | 41 |
| | Abergowrie | 17 | 5.9 | 16.0 | 16 |
| | Black Rock | 7 | 14.3 | 3.0 | 3 |
| | Boyne Island | 26 | 11.5 | 2.3 | 5 |

*Parathelandros mastigurus*, however, has been found to have a wide host distribution across several families of amphibians, including the introduced *B. marinus*, in this study. In addition, *P. mastigurus* infects amphibians over an extensive geographical range of almost 3,000km from Bloomfield (this study) to Sydney (NSW) (Inglis, 1968).

There are no obvious common features of the amphibian species recorded as hosts for *P. mastigurus*. The host species are both terrestrial (*B. marinus, Litoria inermis*) and aboreal (*Litoria caerulea, Litoria rothii*) and are found in rainforest (Mt. Lewis) to open eucalypt woodland (Bentley, Townsville). The life cycle of *P. mastigurus* remains unknown, but other members of the Oxyurida have direct life cycles with either oral infection by embryonated eggs or autoinfection with eggs hatching within the rectum of the host (Anderson, 1992).

Voucher specimens of *P. mastigurus* have been deposited in the Queensland Museum under registration numbers G215994-215999.

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TABLE 2. List of host species examined at geographical locations where *Parathelandros mastigurus* was not recorded. Some of the species listed are also found in Table 1 but were not infected in every geographical location sampled.

| Host species | Geographical location | Number of hosts examined |
|---|---|---|
| *Limnodynastes convexiusculus* | Cape York (Somerset) | 2 |
| *Limnodynastes ornatus* | Townsville | 31 |
| | Abergowrie | 1 |
| | Bentley | 13 |
| | Boyne Island | 1 |
| | Brisbane | 1 |
| | Calvert Hills | 1 |
| | Cape Weymouth | 1 |
| | Cape York (Somerset) | 3 |
| | Coen | 5 |
| | Mountain View Road | 2 |
| *Limnodynastes peronii* | Boyne Island | 6 |
| *Limnodynastes terraereginae* | Boyne island | 3 |
| *Sphenophryne robusta* | Cape York (Somerset) | 2 |
| *Uperoleia lithomoda* | Townsville | 3 |
| *Cyclorana brevipes* | Black Rock | 1 |
| | Coen | 4 |
| *Cyclorana novaehollandiae* | Coen | 1 |
| | Townsville | 1 |
| *Rana daemelii* | Cape Weymouth | 2 |
| *Rana daemelii* | Cape York (Somerset) | 3 |
| *Litoria alboguttata* | Coen | 2 |
| | Mountain View Rd | 1 |
| | Townsville | 15 |
| *Litoria bicolor* | Boyne Island | 3 |
| | Townsville | 5 |
| *Litoria genimaculata* | Paluma | 54 |
| *Litoria lesueuri* | Brisbane | 1 |
| *Litoria nasuta* | Bentley | 2 |
| | Cape Weymouth | 1 |
| | Townsville | 3 |
| *Litoria nigrofrenata* | Cape York (Somerset) | 3 |
| *Litoria rothii* | Black Rock | 1 |
| *Litoria wotjulumensis* | Calvert Hills | 3 |
| *Bufo marinus* | Brisbane | 17 |
| | Calvert Hills | 72 |
| | Cape Weymouth | 42 |
| | Coen | 4 |
| | Charters Towers | 19 |
| | Mackay | 25 |
| | Mareeba | 8 |
| | Port Douglas | 11 |
| | Yungaburra | 10 |

**HOST RANGE EXTENSION FOR *HAEMOPROTEUS COLUMBAE* KRUSE OF PIGEONS AND DOVES (COLUMBIDAE).** *Memoirs of the Queensland Museum 43(2):462. 1999.*- In a survey conducted in cooperation with The Currumbin Wildlife Sanctuary, Gold Coast, Queensland, blood of 40 birds within the avian family Columbidae was collected. Of 6 species examined, 2 species (*Columba livia* and *Leucosarcia melanoleuca*) were found to be positive for the haemosporidian parasite *Haemoproteus columbae*. Prevalence of the parasite in *C. livia* (Domestic Pigeon) was 58% (n=12), often with high intensity, while a single individual of *L. melanoleuca* (Wonga Pigeon) was sampled and positive for the parasite. This is the first record of *H. columbae* in a Wonga Pigeon in Australia.

*Haemoproteus columbae* (Kruse 1890) was described from gametocytic stages in the peripheral blood of *Columba livia* Gmelin. It is a pigmented, halteridial parasite found in the erythrocyte of its host. Host erythrocytes may show hypertrophy and the host cell nucleus may be displaced laterally. The number of pigment granules in the macrogametocyte averages 27 (Bennett & Peirce, 1990), but depends partly on the age of the parasite, with immature gametocytes having fewer than mature gametocytes (Mackerras & Mackerras 1960). Subsequent to Kruse's description of *H. columbae*, 6 additional species of Haemoproteidae were described from the same host family (*H. sacharovyi*, *H. maccallumi*, *H. melopeliae*, *H. palumbis*, *H. piresi*, *H. turtur*) but the validity of some of these species has been questioned (Mohammed 1958; Baker 1966) have questioned . All 7 species were redescribed by Bennett & Peirce (1990) using material from N America, Venezuela, S Africa, India and Zambia (after Kruse's original material of *H. columbae* was lost) and all except for *H. sacharovyi* Novy & MacNeal, 1904 (the only non-halteridial species) were considered to be synonymous with *H. columbae*.

Many of the 320 described species of Columbidae are cosmopolitan in their distribution. For example, *Columba livia* has a distribution which includes Europe, Africa and Asia and has been introduced into many parts of Australia. The distribution of *H. columbae* mirrors that of its hosts in tropical and subtropical areas (Bennett, Garnham and Fallis, 1965) and shows a surprisingly high degree of morphological consistency all over the world (Mohammed, 1958).

In Australia, *H. columbae* has been reported previously in *C. livia* by Wenyon (1926) and by Mackerras & Mackerras (1960) from Western Australia. The latter authors reported gametocytes of 13-15µm long and 4-5µm wide. The parasite did not encircle the ends of the nucleus which was displaced laterally. Infected red blood cells were slightly enlarged.



FIG. 1. Macrogametocyte of *Haemoproteus columbae* from the Wonga Pigeon, *Leucosarcia melanoleuca*.

The second Australian bird species found positive for *H. columbae* was the Superb Fruit-Dove, *Ptilinopus superbus* Temminck, from Townsville, reported by Breinl (1913). The gametocytes were up to 15µm long and 6µm wide. The nucleus was central, pigment in variable amounts, schizonts were not seen probably because the bird was in the chronic stage of infection (Breinl, 1913).

Morphometrics of the material described here are taken from gametocytes in Giemsa-stained thin blood smears. Macrogametocytes (n = 30) in *C. livia* - 11.9µm long 3.25µm wide. Halteridial, occupying more than 50% of the host erythrocyte, margins entire,, nucleus central or subcentral, number of pigment granules 29 (23-35), nuclear displacement ratio 0.54. Infected cells slightly enlarged. Microgametocytes (n= 15) in *C. livia* - *11.1µm long 3.2µm wide. Halteridial, margins* entire, pigment granules 14 (9-18) placed mostly polar, nuclear displacement ratio 0.55. Infected cells slightly enlarged.

In the blood smears of *Leucosarcia melanoleuca* a total of 6 macrogametocytes were found, 3 with highly amoeboid margins, 3 with entire margins, all halteridial, 11.4µm (9.7-12.8µm) long, 2.3µm (1.9-2.6µm) wide, nucleus central, pigment granules 20 (17-22), nuclear displacement ratio 0.81. Poikilocytosis precluded measurement of host cell hypertrophy.

The low number of pigment granules found, compared to Bennett & Peirce's (1990) redescription of *H. columbae* may reflect immaturity of the gametocytes. Apart from this difference, the parasite of *L. melanoleuca* is consistently referable to *H. columbae*.

**Acknowledgements**

We thank the Deutscher Akademischer Austauschdienst (DAAD) for financial support given to RL for her studies.

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# STROMATOPOROID PALAEOECOLOGY AND SYSTEMATICS FROM THE MIDDLE DEVONIAN FANNING RIVER GROUP, NORTH QUEENSLAND

ALEX G. COOK

Cook, A.G. 1999 06 30: Stomatoporoid palaeoecology and systematics from the Middle Devonian Fanning River Group, north Queensland. *Memoirs of the Queensland Museum* **43**(2): 463-551. Brisbane. ISSN 0079-8835.

Thirty five stromatoporoid taxa are described from the Middle Devonian (Givetian) lower Fanning River Group, Burdekin Subprovince, north Queensland, Australia.

Ten faunal communities are recognised, based on the study and distribution of stromatoporoid and selected molluscan taxa, and the distribution of tabulate and rugose corals. The *Burdikinia* community, characterised by robust gastropods, occupied the coarse siliciclastic inner shelf. The *Modiomorpha* community is represented by a near-shore, in situ shell bed. The *Stachyodes costulata-Syringopora* community lived in inner shelf muddy carbonate-dominated lagoons, but was in part able to inhabit subtidal interstitial niches of marine headlands. In the Fletcherview-Burdekin Downs area, the *Hermatostroma maculatum-Gerronostroma hendersoni* community constructed lagoonal patch reefs, back-reef laminar stromatoporoid pavements and bioherms. The *Clathrocoilona spissa-Aulopora* community occupied nearshore, fringing biostromes in the Fanning River area. *Ferestromatopora heideckeri-Amphipora ramosa-Stringocephalus* community occupied extensive nearshore to offshore biostromes within the Fanning River-Golden Valley areas. The *Coenostroma-Hermatostroma episcopale* community dwelt within dispersed stromatoporoid pavements and less commonly, within offshore coralline thickets. The *Amphipora pervesiculata* community characterised by dendroid stromatoporoid-coralline thickets adjacent to and seaward of bioherms, dispersed stromatoporoid pavements and stromatoporoid biostromes, particularly in the Fletcherview-Burdekin Downs area. The *Endoplyllum* community was restricted to patch reefs which grew during a regressive phase, carbonate to siliciclastic transition. A cephalopod association is represented by a sparse fauna occurring within deeper water micritic facies in the Golden Valley area.

Analysis of stromatoporoid shape demonstrates the influence of both genetic and ecologic factors. Zonation of skeletal shape, apparent for both biostromal and biohermal complexes, indicates that strong ecologic influences dominated. Substrate type, sedimentation rate and water depth were important controls. Most taxa display a range of shape. Complex overgrowth phenomena, between stromatoporoid taxa, tabulate corals, chaetetids and algae produced compound skeletons that are most common within nearshore biostromes, and are interpreted to indicate stress imposed by repeated lethal depositional events or by seasonal variations in salinity.

Intergrowths of stromatoporoids with tabulate corals *Syringoporella*? sp. and *Syringopora* sp., a number of rugose corals and a ?vermetid are documented. *Syringoporella*? sp. is more common in stromatoporoids with irregular skeletal architecture. For *Syringoporella*? sp. an even distribution of corallites within the host, skeletal response to corallite occurrence and the absence of micritic envelopes suggests a symbiotic relationship with both the coral and the stromatoporoid accreting at the same rate and maintaining an even growth surface.

Six new species of stromatoporoids are described comprising *Gerronostroma hendersoni, Trupetostroma zheni, Euryamphipora merlini, Ferestromatopora heideckeri, Coenostroma burdekinense* and *Coenostroma wyatti*.

Biogeographic affinities of the fauna are strongly with the Old World Realm, with species level affinities with Guangxi, Poland and Belgium. ❐ *Stromatoporoids, taxonomy, north Queensland, Middle Devonian, palaeoecology.*

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Stromatoporoids are major faunal elements of the ?Eifelian-Givetian Fanning River Group, which cropsout extensively within the Burdekin Subprovince, Townsville hinterland, north Queensland. This study examines the ecology and systematics of the stromatoporoid faunas.

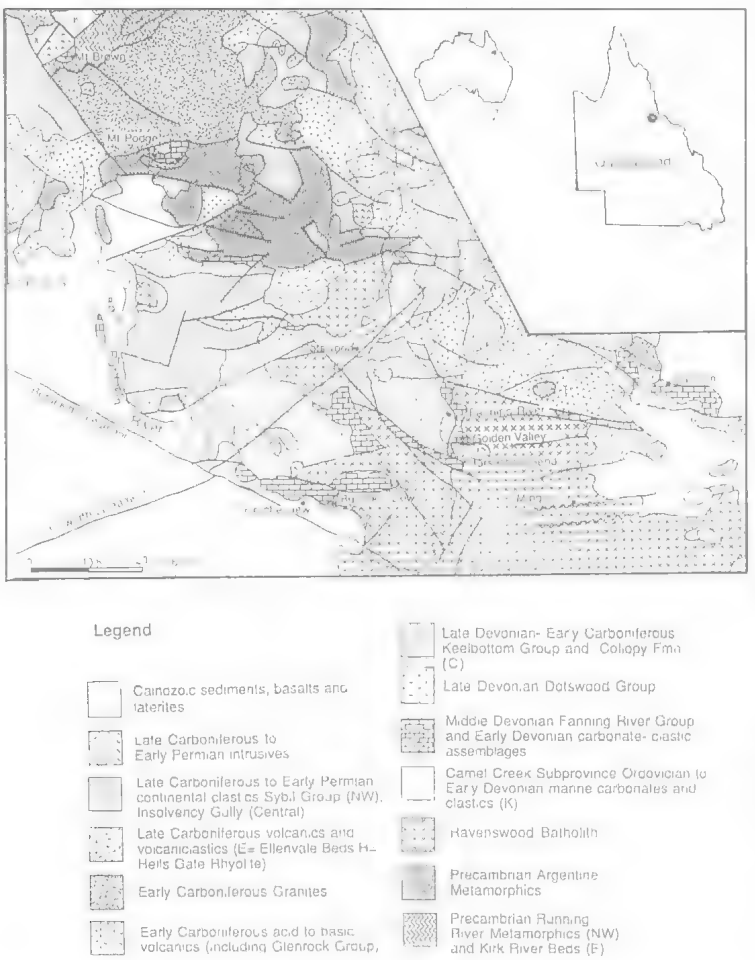



FIG. 1. Geological map of the Burdekin Subprovince after Lang et al. (1990).

The Fanning River Group is the lowermost stratigraphic unit of the Burdekin Subprovince, a Middle Devonian to Carboniferous succession WSW of Townsville (Fig. 1). The Group consists of 3 formations; Big Bend Arkose, Burdekin Formation and Cultivation Gully Formation. In a recent sedimentological study (Cook, 1995), 12 distinct facies have been identified from the Middle Devonian, ?Eifelian-Givetian Big Bend Arkose and Burdekin Formation, of the Fanning R. Group. They represent deposition within the restricted Burdekin Basin in non-marine, inner and proximal shallow water marine shelf, and shallow to moderate depth, distal marine shelf environments. Non-marine deposition (unfossiliferous coarse siliciclastic facies) took place within restricted coastal plains, and represents in situ weathering profiles and coastal plain coarse-grained fluvial channel and finer-grained floodplain deposits. Deposition within the inner shelf was complex reflecting local influences of coarse siliciclastic input, inner shelf carbonate production and an across-shelf siliciclastic to carbonate transition. Facies deposited in the inner shelf are: (1) abraded coarse siliciclastic facies representing inundated marine headlands, and coarse siliciclastics representing upper shoreface deposition, (2) fossiliferous sandstone facies deposited on the lower shoreface to subtidal zone, (3) fossiliferous siltstone facies, representing restricted fine-grained siliciclastic-dominated, nearshore, subtidal embayments, (4) nodular limestone facies deposited within mostly subtidal, carbonate-dominated, impure lagoons with local patch reef development, (5) impure limestone-sandstone facies representing sporadic deposition of mobile coarse siliciclastic sand bodies within impure, subtidal carbonate lagoons. Deposition on the proximal shelf was dominated by stromatoporoid biostromal facies (seven divisions) representing biohermal (reefal) deposition (framestone), back-reef or intra-biostromal stromatoporoid pavement (coverstone), interreef channel (grainy floatstone), and extensive biostromes and storm-reworked equivalents which developed from the nearshore zone across the shallow shelf (silty rubbly floatstone, micritic stromatoporoid floatstone, rudstone, associated packstone and wackestone). Reef and biostromal growth took place during moderate levels of siliciclastic input, in close proximity to the granitic hinterland and can be considered as preserved 'fringing' reef and biostrome. Additionally where extensive reef or biostrome did not develop, the proximal shelf was inhabited by dispersed stromatoporoid pavements (dispersed stromatoporoid packstone facies). Three facies

represent distal shelf deposition, seaward of biohermal or biostromal growth: (1) coralline packstone, representing shallow water, offshore, coral and dendroid stromatoporoid thickets, (2) localised crinoid grainstone deposited as mobile carbonate sand bodies on the shallow distal shelf removed from significant siliciclastic input, (3) micritic carbonate facies, restricted to the Golden Valley area, representing relatively deeper water deposition at the limits of the photic zone. *Endophyllum* siltstone facies represents growth of small, coral-dominant patch reefs in a fine-grained mixed carbonate-siliciclastic environment during initial stages of regression in the uppermost Burdekin Formation within the Fanning R. area.

Deposition was controlled by basement topography and restricted basin geography with significant variations across the subprovince. For a review of the stratigraphy see Draper & Lang (1994), or Cook (1995).

Stromatoporoids are dominantly found within the Burdekin Formation, which based on the conodont studies of Talent & Mawson (1994) has been assigned a mostly Givetian age; see also Cook (1995).

Localities mentioned in this report are detailed in Cook (1995). Material is deposited at James Cook University of North Queensland, with a small collection at the Queensland Museum. Prefixes used in this work are JCUL for James Cook University geological locality and JCUF for James Cook University Fossil collection.

## PREVIOUS PALAEONTOLOGICAL STUDIES

Palaeontological investigations of the Fanning River Group commenced with the work of Clarke (in Leichhardt 1847) who described '*Cyathophyllum leichhardti*' from the Burdekin River. Nicholson & Etheridge (1879), Etheridge (1880), Etheridge & Foord (1884), Jack & Etheridge (1892) and Etheridge (1917a, 1917b) all contain descriptions and lists of fossil collections from the Burdekin. Nicholson & Etheridge (1879) also described a number of tabulate corals from the Fanning R. and Arthurs Ck areas. They also briefly documented the presence of *Stromatopora* and *Caunopora* from Arthurs Ck, representing the first record of stromatoporoids from the Burdekin. Etheridge (1880) described 5 brachiopod taxa from the Fanning R. area collected by Robert Logan Jack. Etheridge & Foord (1884) described 2 coral taxa and one chaetetid taxon from the Reid's Gap area.

Jack & Etheridge (1892) described and illustrated many faunal elements from the Burdekin Formation as part of the monograph on the Geology and Palaeontology of Queensland. Included were the first description and illustrations of stromatoporoids from the region with *Stromatopora* described and illustrated and *Stromatoporella* illustrated but not described. Etheridge (1917a) erected the gastropod species *Polyamma burdekinensis* subsequently revised by Knight (1937) and Heidecker (1959). Etheridge (1917b) described the polyzoan *Vetofistula miribalis* from the limestones at Reid's Gap, but this has subsequently been referred to as a species of the tabulate coral *Cladopora* (Hill 1981).

Hill (1942) made a detailed study of the rugose corals from 3 localities in the Burdekin Subprovince; Fanning R., Burdekin Downs and Reid's Gap. She illustrated and described 23 species of rugosans and mentioned the ramose stromatoporoid *Amphipora*, the brachiopods *Atrypa* and *Stringocephalus*, and the gastropod *Polyamma*. She also assigned a mid-Givetian age to the beds based on their similarities to European faunas. Brown (1944) briefly described *Stringocephalus burtini* Defrance from Fanning R. and Reid's Gap, also attributing a Givetian age to the limestone units. Heidecker (1959) described 4 molluscan genera (1 bivalve and 3 gastropods) of which 3 were new, from the Big Bend Arkose and Burdekin Formation near Lowes Basin. In Hill, Woods & Playford (1967) an unnamed stromatoporoid and a number of molluscan, rugose coral and tabulate coral taxa from the Burdekin Formation were illustrated. Strusz (1969) and Strusz & Jell (1971) discussed rugose coral taxa from the Fanning R. Group. West (1974) recognised 3 informal biostratigraphic zones as part of a study of the rugose corals at Fanning R. : the *Temnophyllum* sp. nov. range zone, the *Stringophyllum* sp. cf. *quasinormale* assemblage, and the *Endophyllum abditum columna* range zone. West (1974) inferred an early- to mid-Givetian age for the sequence but qualified the utility of these zones with a discussion of the facies dependence of the coralline forms. In addition, West (1974) mentioned and illustrated a number of tabulate corals and *Amphipora* spp. Stephenson (1977) documented a number of rugose and tabulate corals from the Fletcherview area. Henderson (1984) discussed the diagenetic origin of silica

within a 'Hermatoporoidea' type stromatoporoid from Fanning R. A major study of the rugose coral fauna was undertaken by Zhen (1991) who identified 10 coral assemblages within the Fanning R. Group *sensu lato*, comprised of 79 species and subspecies distributed amongst 41 genera of rugose coral. Zhen (1991) provided the basis for rugose coral identifications given in the present work. He briefly noted the presence of some stromatoporoid taxa, but did not attempt their systematic evaluation. Jell et al. (1988) recorded the crinoid taxon *Cupressocinites abbreviatus* Goldfuss from Big Bend and an indeterminate crinoid from Herveys Range outcrops of the Burdekin Formation. In more recent times Cook (1993a,b; 1997) has examined molluscs from parts of the Fanning R. Group, and Zhen (1994) and Zhen & Jell (1996) have formalised some of the rugose coral taxa. Zhen & West (1997) described some symbionts in both stromatoporoids and chaetetids from the Burdekin Formation.

## AUSTRALIAN DEVONIAN STROMATOPOROID STUDIES.

Systematic and palaeoecologic work on Australian Devonian stromatoporoids is sparse. Stromatoporoids have been mentioned commonly, listed infrequently and described rarely. To date the works of Ripper (1933, 1937a,b,c,d, 1938), Mallett (1968, 1970a,b, 1971), and Cockbain (1984, 1985), Webby, Stearn & Zhen (1993) and Webby & Zhen (1997) form the main body of Devonian stromatoporoid work.

In Victoria, description of Early Devonian stromatoporoids from Lilydale (Ripper 1933, 1937b), Loyola (Ripper 1937c), Buchan (Ripper, 1937d) culminated in a synthesis of their assemblages by Ripper (1938). She also described '*Amphipora ramosa*' (Phillips) from Western Australia. The Lilydale, Buchan, Tyers and Waratah Bay stromatoporoids were reviewed by Webby, Stearn & Zhen (1993).

Mallett (1968, 1970a,b, 1971) described stromatoporoid faunas from the Broken R. Province. Cockbain (1984) described 25 species of stromatoporoids from the Canning Basin reef complexes, Western Australia. The taxa range in age from Givetian to Famennian. A small fauna of stromatoporoids from the Carnarvon Basin was described by Cockbain (1985). Shorter works include those of Etheridge (1911), Dun (in Benson 1918), Cockbain (1979) and Cockbain (1989). Webby & Zhen (1993) described the Early Devonian allochthonous stromatoporoids of the Jesse Limestone, New South Wales. There are a number publications which list Australian Devonian stromatoporoids, including Benson (1922), Teichert & Talent (1958), and Philip (1960,1962). This summary does not include the large number of minor references that are of little taxonomic value. Several of these are listed in Flügel & Flügel-Kahler (1968). Most recently Webby & Zhen (1997) have published part of their ongoing work on the stromatoporoid faunas from the adjacent Broken R. Province.

## PALAEOECOLOGY

Cook (1995) established 11 marine facies within the Big Bend Arkose and Burdekin Formation providing an ecostratigraphic framework for faunal study. Zhen & Jell (1996) established a broad, basin-wide model for the Fanning R. Group, representing the coral and sedimentologic associations. Here a more detailed ecological roles, inter-relations and responses to different environments of the stromatoporoids and other selected organisms preserved in the Big Bend Arkose and Burdekin Formation will be discussed under 5 headings:

1) Stromatoporoid shape, and shape groupings present in stromatoporoid-bearing facies.

2) Differences in shape groupings between related facies to establish whether zonation exists across reefoid facies, and to investigate which factors most strongly influence stromatoporoid shape.

3) Diversity in shape within individual stromatoporoid taxa.

4) Relationships between stromatoporoids and other organisms, assessed from intergrowth and overgrowth phenomena to determine if inferences of the physical environment can be made from such characteristics.

5) Community groupings of stromatoporoid and other faunal elements, their partitioning and overlap, their guild structure, and the role of individual taxa within the guild structure.

In addition the palaeobiogeographic affinities and relationships of the fauna are also discussed.

## STROMATOPOROID SHAPE

Stromatoporoid shape was controlled by both ecologic and genetic factors (Kapp, 1975; Kershaw & Riding, 1980; Kershaw, 1981, 1984, 1990; Stearn, 1982a; Kano, 1990). Analysis of

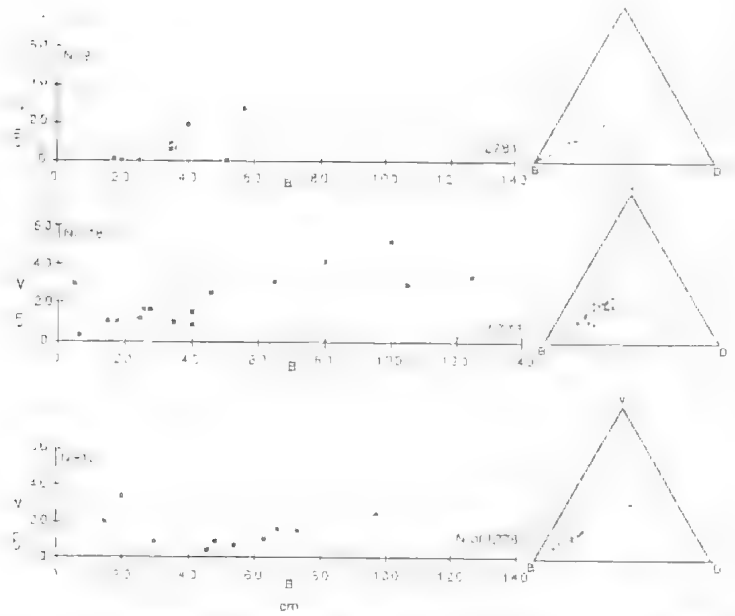


FIG. 2. Stromatoporoid skeletal morphology from patch reef environments of the Burdekin Formation. Bivariate plots show vertical height (V) versus basal width (B) in centimetres. Triangular plots show vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°. A, L781 patch reef approximately 23m above base of section. B, L778 patch reefs approximately 13m above base of section. C. Patch reef in spot exposure of facies approximately 1km N of L778.

skeletal growth shape may provide useful insights into the palaeoecology of fossil reefal and biostromal organisms, but there is little consensus on the precise influences of environmental conditions on shape. Many authors have made palaeoecological inferences based on the study of both gross colonial shape in relation to substrate (Kapp 1975, Kershaw & Riding 1978, Kershaw 1981, 1984, 1990, Bjerstedt & Feldmann 1985, Kano 1990), and relationships of colony margins to enclosing sediments (Broadhurst, 1966; Kapp, 1975; Kershaw & Riding, 1978; Kershaw, 1984). Several authors have argued for lateral and vertical zonation within stromatoporoid-bearing strata (Kobluk, 1975; Bjerstedt & Feldmann, 1985) and some have attempted to relate stromatoporoid shape groupings, to combinations of ecological conditions such as oxygenation, turbulence, and sedimentation rate (St Jean, 1971; Bjerstedt & Feldmann, 1985; Kano, 1990; Kershaw, 1990).

For a qualitative assessment of stromatoporoid shape it is important to maintain consistent terminology. Gross skeletal terminology has been developed by many authors including Broadhurst (1966), Abbott (1973), Kershaw & Riding (1978), Cockbain (1984), and Kano (1990). In this, and the following chapter dealing with the systematic descriptions of the fauna, the terminology of Kershaw & Riding (1978) is used, with the addition of 2 terms introduced by Cockbain (1984): 'stachyodiform' and 'amphiporiform'. Thus the terminology used herein is: laminar (with a height to base ratio < 1:10), low domical, medium domical, high domical (extended domical of Kershaw & Riding (1978)), bulbous, irregular, dendroid comprising stachyodiform and amphiporiform.

Some authors (e.g., Kobluk, 1975; Kano, 1990) have attempted to graphically display the size groupings of stromatoporoids by use of a simple plot of width versus height. Although the procedure gives a good indication of size it was noted that it does not adequately quantify the shape of the organisms, leading Kershaw & Riding (1978) to parameterise stromatoporoid shape using percentile ratios of vertical height (V), basal width (B) and diagonal distance (D) at a set angle (q) plotted on a triangular diagram or triplot. For comparative purposes, their method provides a simple, quick, graphical display of shape domains within facies or communities. Kershaw & Riding's (1978) approach is quite useful in indicating the shapes of large, regular stromatoporoid skeletons and those of other groups. However the method has the following disadvantages: (1) There is no dimensional scale for the skeleton. (2) The entire field on the triplot is never represented as some forms are unattainable in stromatoporoids. (3) The method does not adequately represent dendroid forms and does not deal with irregular forms. (4) The method requires either full specimen collection, generally impossible with the Burdekin fauna, correction of 'oblique' data , or excellent, vertically exposed sections through the centres of skeletons.

Nevertheless the triplot method of representing shape domains is a useful benchmark with which to compare stromatoporoid occurrences and combined with the more traditional base versus height plots, and provides a useful graphical characterisation for the assemblages. Data were collected from representative stromatoporoid-dominant facies to characterise the general shapes domains of the non-dendroid stromatoporoid fauna. Field measurements were made with a simple measuring tape, reading to the nearest 0.5cm.

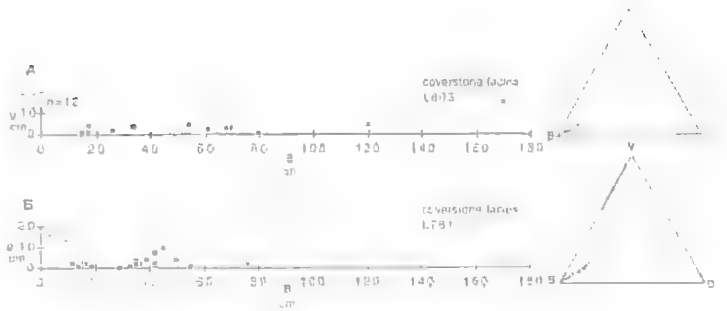



FIG. 3. Stromatoporoid skeletal morphology from coverstone facies of the Burdekin Formation. Bivariate plots show vertical height (V) versus basal width (B) in centimetres. Triangular plots show vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°. A, L803, uppermost facies exposed within Ropeladder Cave. B, L781, facies immediately underlying biohermal unit.

STROMATOPOROID SHAPE WITHIN PATCH REEFS. Two types of patch reefs were identified within the nodular limestone facies by Cook (1995); columnar, bulbous or pillar shaped reefs and diffuse patches of coverstone-framstone.

Both types show a dominance of large, low domical forms (Fig. 2) with very few high domical and bulbous forms. For the loosely bound, framestone and coverstone style of patch reefs these shapes can be attributed to the need for the stromatoporoid to grow more quickly laterally than vertically across a muddy substrate for support, thus distributing the weight across a larger surface area. This phenomenon has been noted by several authors (Meyer, 1981; Bjerstedt & Feldmann, 1985; Fagerstrom, 1987; Kano, 1990). The strategy was called the 'snow-shoe' approach by Bjerstedt & Feldmann (1985). Within the 'rauk' patch reefs the stromatoporoid skeletons are individually dominated by low domical forms, but their superposition creates the high relief profile of the patch reef. Away from these patch reefs and commonly in haloes around them, dendroid, mostly stachyodiform elements of the fauna are common.

STROMATOPOROID SHAPE WITHIN LAGOONAL PAVEMENTS. A number of coverstone occurrences were interpreted as lagoonal pavements either leeward of bioherms or within a biostromal complex (coverstone subfacies (Cook, 1995)). These pavements are almost exclusively composed of laminar to very low domical stromatoporoids (Fig. 3). Skeleton edge raggedness suggests moderate sedimentation rate (Broadhurst, 1966; Tsien in Stearn 1982a; Bjerstedt & Feldmann, 1985), which could not have exceeded rates within the nearer shore lagoons supporting patch reefs. Indeed, in the coverstone facies of L803, the laminar dominant forms occur at the top of an energy waning cycle suggesting a relative reduction in sedimentation. Control by substrate-type in addition to sedimentation rate is indicated, with growth forms reducing their weight per unit area (Kershaw, 1984; Bjerstedt & Feldmann, 1985; Kershaw, 1990). Some of the laminar forms in these occurrences are spectacularly thin in comparison to their width (Fig. 3). St Jean (1971) suggested that thin laminar forms occurred in oxygen poor conditions, but as Bjerstedt & Feldmann (1985) have argued, a laminar form would be at a disadvantage in such circumstances with the living surface close to the sediment-water interface. Furthermore, the extensive bioturbation, and the presence of molluscs and brachiopods suggest a moderately well-oxygenated benthos at L803.

Robustly dendroid skeletons are abundant in lagoonal pavement facies, attesting to the importance of the dendroid form in mud-dominated substrates. Bjerstedt & Feldmann (1985) argued that fasciculate skeletons are disadvantaged within this environment. Clearly the abundance of dendroid forms within the muddy facies of the Burdekin Formation refutes this argument. On the contrary, dendroid skeletons would be able to raise the living surface well above the sediment water interface. The only problem is

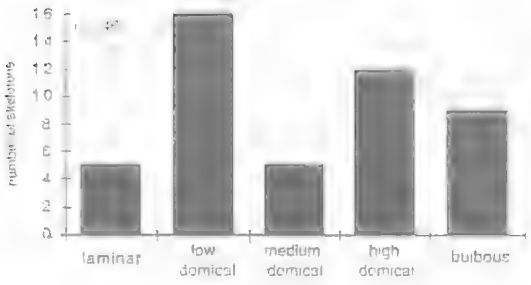



FIG. 4. Histogram showing proportions of gross skeletal shapes for compound skeletons from biostrome within fossiliferous siltstone facies at L788, approximately 16m above base of section.

to provide a substrate upon which to initially colonise, but the abundant small bioclasts of molluscan hash, small corals and other millimetre-scale debris would have been sufficient. As sedimentation progressed, the dendroid skeleton, becoming progressively more buried in the substrate, would gain stability.

STROMATOPOROID SHAPE WITHIN BIOSTROMAL OCCURRENCES. Several types of biostrome were identified by facies analysis in Cook (1995). These are generally the innermost shelf biostromes of the fossiliferous siltstone facies typically represented at L788, and the extensive proximal shelf biostromes represented throughout the Fanning R. area.

(1) Innershelf biostrome (JCUL788)

Study of this biostrome revealed that it was loosely bound, enclosed by dominantly siliciclastic facies, and formed in a shallow, subtidal environment, situated extremely close to shore in a restricted embayment with a moderate sedimentation rate as suggested by the sandy stringers and interbeds. In many ways this small biostromal lens, and the overlying 5 metres of stromatoporoid-bearing sequence, is one of the most instructive in the Burdekin sequences as it occurs in a facies with between 60 and 70% siliciclastic component (determined by bulk acid dissolution of several samples).

The dominant (>75%) gross skeletal shape is irregular, consisting of many compound forms with laminar and high domical components to the one skeletal unit. Others are multiply bulbous, arising from a low domical form. Of the 63 skeletons assessed in this biostrome only 48 could be assigned confidently to an approximate skeletal shape category (Fig. 4) and the size of the skeletons is highly variable. Unfortunately preservation is very poor, with much skeletal silicification, neomorphism and minor dolomitisation, rendering the taxonomy of this faunule difficult. The skeletons present are quite distinct from others in the Burdekin succession. The majority are compound, composed of repeated, variably thin layers of encrusting organisms including stromatoporoids, alveolitids and algae (see below). Their compound nature may explain the aberrant growth forms of the skeletons. If a single taxon adopted a limited and related range of growth forms (see below), then the superposition of many taxa in an encrusting relationship may be expected to produce a highly irregular form. Thus the skeletal form of most individual taxa within this biostrome is laminar, with thin encrustations complexly overgrown to form irregular compound skeletons. Away from, and within, the biostrome dendroid (mostly tabulate coral) skeletons are very common.

(2) Proximal shelf biostrome.

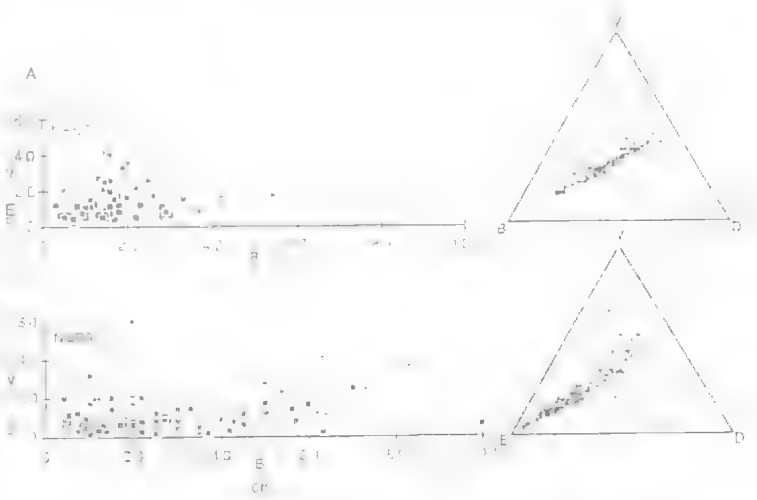



FIG. 5. Stromatoporoid skeletal morphology from proximal shelf biostromal facies of the Burdekin Formation. Bivariate plot showing vertical height (V) versus basal width (B) in centimetres. Triangular plots showing vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°. A, L788 26m above base. B, L788 87m above base.

Stromatoporoids from the proximal shelf biostromal facies at L788 show a wide range of shapes and sizes, but with a general dominance of low to high domical forms, sporadic bulbous forms, and a lower proportion of laminar forms (Fig. 5) in comparison to the inner shelf. Compound skeletal phenomena are much less common. There are large numbers of fragmental skeletal remains within reworked facies but it is obvious that the unreworked facies do represent the stromatoporoid populations adequately.

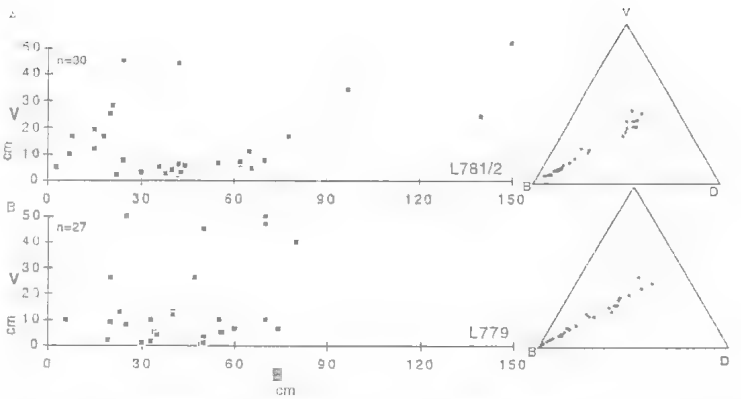



FIG. 6. Stromatoporoid skeletal morphology from proximal shelf framestone facies of the Burdekin Formation. A, vertical height (V) versus basal width (B) in centimetres for L781/2 and L779. B, triangular plots of vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°.

Of the larger stromatoporoid skeletons, many show directional growth changes, probably the result of in vivo reorientation. The marked dominance of higher forms in some units of the micritic stromatoporoid floatstone (Fig. 5) may indicate lower sedimentation rate, or a slightly reduced ambient energy (turbulence) away from shoreline. Bioturbation and the abundance of brachiopods negate low oxygen conditions. Sufficiently low energy ambient conditions coupled with a lower sedimentation rate on the mid-shelf would have enabled higher forms to be maintained on the substrate. Inability of some higher stromatoporoid skeletons to maintain a foothold may account for all the regrown high domical stromatoporoids in the facies with reorientation due to sporadic toppling.

Interstitial stachyodiform and amphiporiform taxa play a major role in the biostromes, with *Amphipora* dominating the muddy substrate, occupying patches between the larger stromatoporoids. In addition *Stachyodes costulata* is found as detached branches and as branches originating from an encrusting surface, demonstrating change in growth form within the one skeleton. There are no recorded attachment or encrustation habits of *Amphipora.* Perhaps this is a function of a small size of the attachment surface or perhaps the method of attachment was purely soft-part, but the latter possibility seems unlikely given the ability of *Euryamphipora* to encrust. Both dendroid taxa were successful between the larger stromatoporoid skeletons where they were sheltered, and able to raise the living tissue well above the substrate.

STROMATOPOROID SHAPE WITHIN BIOHERMS (REEFS). Well exposed outcrops of stromatoporoid framestone along the Burdekin R. (L779, L781, L782) allow for a sizeable analysis of stromatoporoid shape domains. The bioherm is dominated by low to medium domical forms (Fig. 6), many wider than 1m, and higher than 50cm. There is a general reduction in the number of high domical and bulbous forms in comparison to the biostromal facies in the Fanning R. area which may be a function of higher energy at the reef top, and the general difference in the stromatoporoid taxa between the 2 areas. Whilst common, the dendroid fauna is less abundant than in flanking environments, restricted to interskeletal niches.

STROMATOPOROID SHAPE WITHIN DISPERSED STROMATOPOROID PAVEMENTS AND OFFSHORE THICKETS. These environments were completely dominated by *Amphipora* and/or ramose tabulate coral taxa, and the role of the non-dendroid stromatoporoids was minor on the distal shelf. Growth form was variable, with some facies dominated by thick laminar and low domical forms (Fig. 7), both with and without ragged margins, and other occurrences showing sporadic medium and even high domical forms. The thick laminar and low domical forms occur in the dispersed stromatoporoid packstone facies which, given the abundance of micrite presumably derived from algae, would have been a highly productive carbonate factory where carbonate accumulation was relatively high, the overall substrate

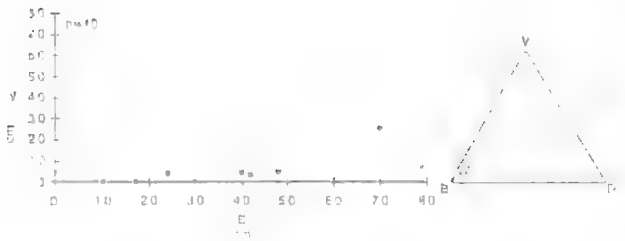


FIG. 7. Stromatoporoid skeletal morphology from dispersed stromatoporoid and coralline packstone facies of the Burdekin Formation. Bivariate plot shows vertical height (V) versus basal width (B) in centimetres. Triangular plots show vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°. L781 units above framestone facies.

relatively soft, but with much millimetre-scale skeletal debris available on which to initially encrust. Sporadically preserved raggedness within higher forms of the coralline packstone facies suggeststhat these skeletons kept pace with carbonate accumulation following initial rapid lateral growth.

STROMATOPOROID SHAPE WITHIN SILTSTONE MICROATOLLS. Many stromatoporoids within this facies are encrusting in habit, thus having a laminar form, but there are a few low to medium domical forms, and sporadic high domical forms. *Clathrocoilona spissa* has an irregular, laminar shape in this facies. *Salairella buecheliensis* and *Stromatopora huepschii* show low to medium, rarely high, domical skeletons. The varying microenvironments around such *Endophyllum* accumulations would account for much morphological variation, and the laminar (encrusting habit) forms would result from strong competition for substrate control within an increasingly clastic environment.

## SHAPE ZONATION

BURDEKIN RIVER. Laminar forms in the coverstone facies of L779, and L781/2 are vertically succeeded by low-medium domical forms of the biohermn facies. This vertical zonation is strikingly obvious (Fig. 8) and cannot be related to faunal differences as the stromatoporoid taxa are common to both facies and dominated by *Hermatostroma maculatum* and *Gerronostroma hendersoni*. The progression is interpreted as one of self-generating change in the available skeletal substrate. As the number of large skeletons increased, the skeletal substrate available for colonisation was enhanced, increasing the potential for frame-building. Thus the transition from laminar to domical dominant facies reflects the development from an encrusting pavement to a framework. A reduction is sedimentation rate is possible, but would have been affected by the development of a framework and the consequent elevated growth form of the reef surface from the surrounding substrate. Any change in turbulence would also result primarily from reef growth, rather than vica versa. Thus the major control on morphological change is substrate availability, with a feedback relationship between substrate and skeletal morphology.

FANNING RIVER CAVES. Brief mention has already been made in Cook (1995) of the sequence exposed in Fanning R. Caves (L803). The sequence is interpreted as a waning cycle commencing with a boulder rudstone zone composed entirely of reworked skeletons, an upper boulder rudstone with occasional in situ skeletons, a shingle zone with pebble- to cobble-sized reworked skeletons and many in situ skeletons with ragged margins, and an upper wackestone-coverstone zone dominated by extreme laminar forms. The shape progression in the upper 3 zones (Fig. 9) shows a reduction in the profiles of stromatoporoid skeletons mirroring the reduction in coarse skeletal debris, and hence hydrodynamic energy. Collection of material for taxonomic analysis was not possible as the caves are environmentally sensitive. However it is clear

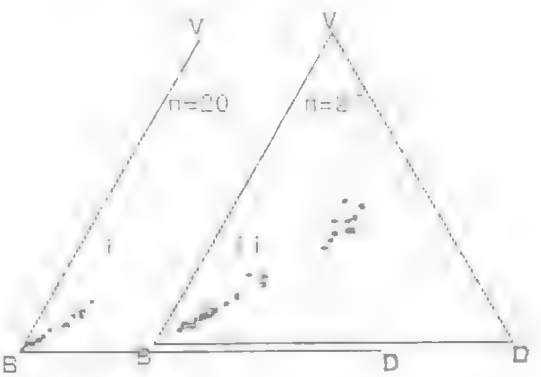



FIG. 8. Stromatoporoid shape domains using VBD triplot for coverstone to framestone facies L781.

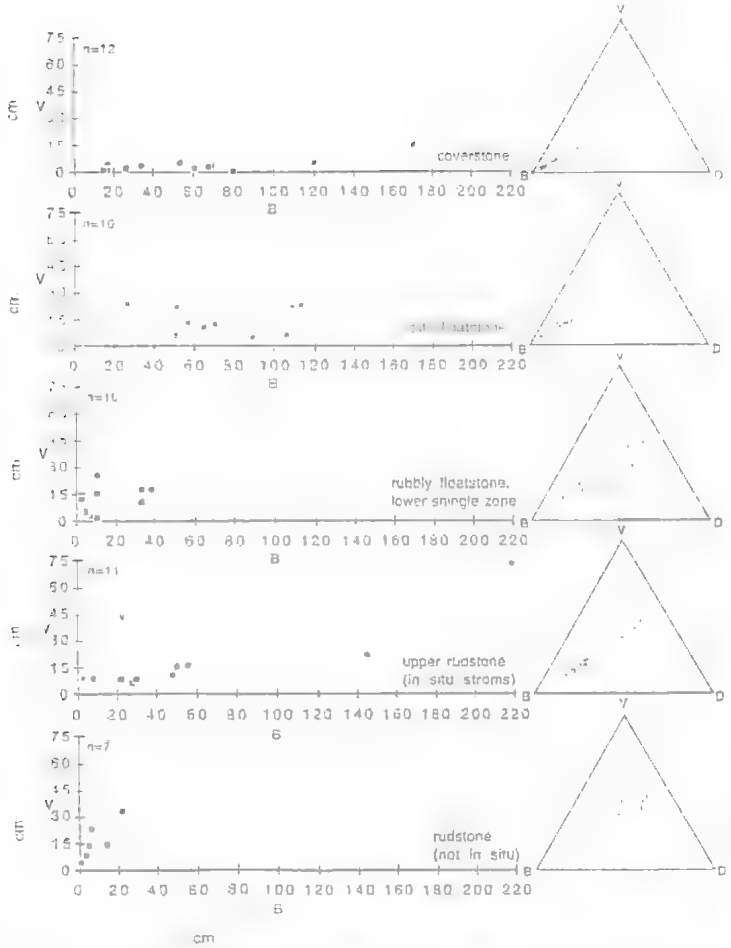



FIG. 9. Stromatoporoid shape change for measured section in Fanning River Caves L803 demonstrated in gross skeletal shape plots for each unit (coverstone at top).

from field inspection that there was no obvious change in the faunal constituents. The obvious change in gross skeletal shape demonstrates that here decreasing energy favours lower skeletal profiles. Bioturbation rules out the possibility of an oxygen-poor substrate and the thin forms can be attributed to moderate rates of sedimentation which periodically smothered the organisms.

## STROMATOPOROID SHAPE AND TAXA

Stromatoporoid taxa within the Fanning R. Group display a range of shapes for individual taxa (Fig. 10). Most taxa, of which *G. hendersoni* is an example, are restricted to the low domical and adjacent growth forms. *G. hendersoni* is low to medium domical in form within the bioherm and biostromes, but is laminar to very low domical in coverstone facies. Similarly *Hermatostroma maculatum* is laminar in coverstone facies and low-medium domical in the biohermal complex. Some taxa display a wide range of growth forms, from laminar to bulbous and irregular within the same facies. *Stachyodes costulata* had coexistent laminar, irregular and stachyodiform growth, indicating that it arose from an encrusting surface. Other taxa such as *Hermatostroma episcopale,* strongly restricted to particular facies, are almost exclusively of one shape (laminar, less commonly low domical). Given that individual taxa display a range of shapes across, and within, specific environments, these data show there is very weak genetic control in addition to environmental controls outlined below.

## CONTROLS ON SHAPE

The nature of the muddy substrate and the rate of sedimentation were fundamental determinants of skeletal shape within the inner shelf. Progression from laminar forms to low domical forms reflected in the transition from lagoonal pavement to bioherm was controlled by the increasing availability of skeletal substrate. In the biostromal complex, innermost dwellers had their irregular shape controlled by the sedimentation pattern, the encrusting strategy of the dominant taxa and the dominance of skeletal substrate. In the proximal shelf biostrome higher skeletal form reflected the quiet ambient conditions, sponsoring some toppling and regrowth.

## OVERGROWTH RELATIONSHIPS

Although encrustation of individual stromatoporoid skeletons by other stromatoporoids and a range of other organisms is common, the phenomenon has been given little direct attention (Kazmierczak, 1971; Neild, 1986; Fagerstrom, 1987; May, 1993), although numerous authors have

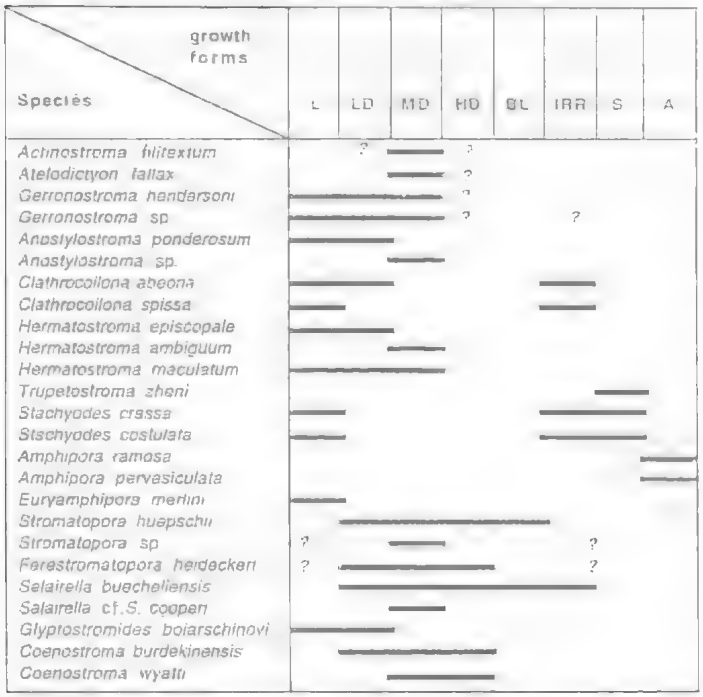



FIG. 10. Gross skeletal shape ranges of major stromatoporoid taxa in the Burdekin Formation. L = laminar, LD = low domical, MD = medium domical, HD = high domical.

noted encrusting forms (Kobluk, 1975), habits and strategies. Many skeletons preserved within Devonian (and other) reefoid systems are compound units, made up of the superposed or overgrown skeletons of a number of organisms. These taxa are preserved either encrusted on the terminal surface of one taxon or included within the skeleton and later overgrown by regrowth of the original host or a subsequent encrusting organism. Kazmierczak (1971) interpreted 2 different surfaces within stromatoporoid skeletons: growth inhibition surfaces such as latilaminae bases, inclusion and regrowth surfaces and growth interruption surfaces such as those marked by encrusting tabulate corals. In the present work 2 types of surfaces are recognised with the encrusting relationships of biohermal and biostromal organisms (mainly stromatoporoids) of the Fanning R. Group. These are growth termination surfaces and growth interruption surfaces.

Growth termination surfaces are those within a compound skeleton which indicate that the older host has been completely encrusted by another organism. A growth interruption surface is a surface which shows partial encrustation of another taxon, but subsequent regrowth of the original host, or some other feature such as a latilamina base, which indicates a non-fatal growth pause.

The main skeletal encrusters, as distinct from sediment binders within the Fanning R. Group are: 1, Stromatoporoids: particularly *Clathrocoilona spissa*, *C. abeona*, *Stromatopora* sp., *S. huepschii*, *Gerronostroma* sp., *Ferestromatopora* sp., *Salairella buecheliensis*, and to a lesser degree *Hermatostroma maculatum*, *Gerronostroma hendersoni* and *Stachyodes costulata*. 2, Tabulate corals: foliose *Alveolites* sp., reptant *Aulopora* sp., and rare *Heliolites* sp. and *Aulostegites* sp. 3, Chaetetids: *Litophyllum koninckii*. 4, algae.

Most stromatoporoid skeletons within the Fanning R. Group are simple, consisting of 1 or 2 growth episodes with perhaps an encruster such as *Aulopora* sp. on the terminal surface. However it was initially observed that some facies contained a disproportionate number of compound skeletons which were more complex accumulations of many generations of encrusters in comparison to other stromatoporoid-bearing facies. In particular biostromes associated with the fossiliferous siltstone facies and lowermost silty rubbly biostrome facies included a high proportion of compound and irregular skeletons. To quantify this observation skeletons from 4 main biostromal and biohermal facies were surveyed in the field, in hand specimen and thin section, and ascribed to the following divisions of skeletal complexity:

a) simple skeletons; containing 1 or 2 taxa or growth phases with or without a minor terminal encrustation of auloporid coral.

b) skeletons of limited complexity; composed of 3 or 4 encrustations or growth phases

c) moderately complex skeletons containing between 5-7 phases of encrustation

d) extremely complex skeletons composed of more than 7 phases of encrustation.

Figure 12 highlights the large proportion of extremely complex skeletons within lowermost biostromes in the Fanning R. area (L788) whereas the most simple skeletons predominate in the

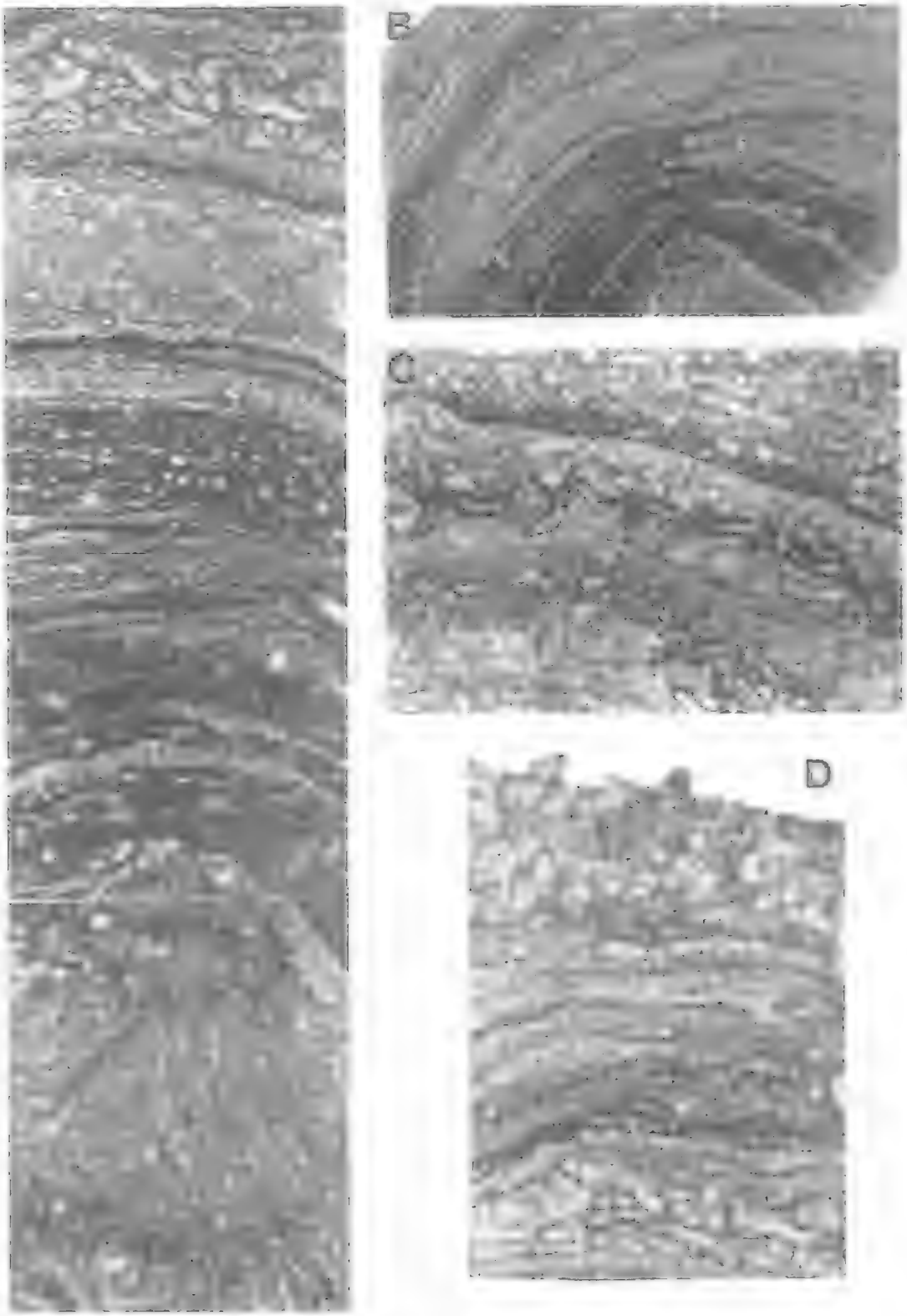



FIG. 11. A-D, thin sections of compound, complex skeletons from biostrome at L788/16m showing repeated overgrowths of stromatoporoids, tabulate corals and micritic seams ascribed to endolithic algae. A, D, F11426, × 5; B, F11426, × 2; C, F11430, × 5.

TABLE 1. Growth phase thicknesses for selected compound skeletons from the L788/16m nearshore biostrome.

| Specimen JCUF | No. of phases | Thicknesses in mm | Taxa present |
|---|---|---|---|
| 11420 | 7 | 10, 9, 9, 2, 4, 10, 7 | *Stromatopora* sp., *Clathocoilona spissa* |
| 11425 | 5 | 12, 3, 7, 6, 2 | *Stromatopora* sp., *Clathocoilona spissa*, *Litophyllum* sp. |
| 11423 | 8 | 1, 4, 1, 1, 7, 2, 7, 2 | *Stromatopora* sp., *Clathocoilona spissa*, *Aulopora* sp. |
| 11430 | 6 | 5, 3, 5, 6, 3, 3 | *Stromatopora* sp.,*Clathocoilona spissa*, *Aulopora* sp. |
| 11426 | 14 | 14, 1, 1, 5, 3, 6, 2, 2, 2, 3, 4, 3 | ?*Stromatopora* sp., *Clathocoilona spissa*, *Aulopora* sp. |
| 11418 | 11 | 3, 3, 2, 6, 3, 6, 4, 5, 7, 2, 4 | *Stromatopora* sp. , *Aulopora* sp., *Clathrocoilona spissa* |
| 12772 | 13 | 18, 2, 3, 8, 2, 4, 15, 4, 1, 1, 2, 1 | *Litophyllum* sp, *Stromatopora* sp, *Aulopora* sp., *Clathrocoilona spissa* |
| 12773 | 9 | 20, 1, 5, 4, 3, 4, 5, 6, 8 | *Stromatopora* sp. , *Aulopora* sp., *Clathrocoilona spissa*, *Alveolites* sp., ?*Gerronostroma* sp. |
| 12774 | 15 | 4, 3, 1, 3, 2, 12, 2, 1, 3, 1, 2, 4, 5, 5, 3 | *Clathrocoilona spissa*, *Stromatopora* sp., Alveolites sp., *Aulopora* sp. |
| 12775 | 10 | 2, 3, 4, 2, 2, 2, 1, 1,.4,.1 | *Clathrocoilona spissa*, *Stromatopora* sp., *Aulopora* sp. |
| 12776 | 11 | 3, 8, 1, 2, 2, 2, 2, 3,.2, 6, 6 | *Stromatopora* sp. , *Aulopora* sp., *Clathrocoilona spissa* |

biohermal facies of the Burdekin Downs area (L781).

Skeletons in the lowermost biostrome within the fossiliferous siltstone facies are referred to the *Clathrocoilona spissa-Aulopora* community. Skeletons are not only internally complex (Fig. 11), but also show a high degree of irregularity in gross shape. Phases of organism growth are thin, generally less than a few centimetres (Fig. 11, Table 1). This suggests that each growth phase was relatively short-lived. Termination surfaces between these phases are commonly marked by a thin dark micritic seam (Fig. 11) interpreted as having been produced by endolithic algae on the bare skeletal surface. By contrast the amount of sedimentary particles included between growth phases is relatively low. There is some marginal raggedness and sediment inclusion (Kershaw & Riding, 1978) but this is no more pronounced than in other facies, and many of the compound skeletons have an enveloping structure (*sensu* Kershaw & Riding, 1978). The biostrome in which these skeletons lived was a low-relief, poorly-bound pavement which developed adjacent to shore in a restricted, wholly subtidal, essentially siliciclastic environment. Acid residue analysis indicates that the siliciclastic component constituted between 60 and 70% of the enclosing detrital sediment of this facies, compared with variable, but much lower values for detrital sediment associated with other stromatoporoid-bearing facies (Table 2). Each encrustation phase within these complex skeletons represents a terminal surface. Extreme thinness of the growth phases suggests that they were relatively short-lived, or slow growing due to stress. Skeletons experienced succession of short-lived encrustations punctuated by fatal conditions resulting from extreme stress.

Given the low frequency of sediment inclusions, these repeated fatal conditions are unlikely to result from suffocation by detrital sediment. In addition the abundance of the micritic seams supports the view that fatal conditions were succeeded by a period of skeletal exposure facilitating endolithic algal growth.

By analogy with similar phenomena in modern coralline systems under stress, these conditions were probably related to water quality conditions such as brackish water or hypersalinity. Given the much less common occurrence of complex skeletons in other facies, which have subdued siliciclastic signatures, the conditions were probably related to nearshore sedimentation, further suggesting spasmodic influxes of brackish water. Hence this biostrome is interpreted as a repeatedly stressed benthic community which was capable of quick regeneration. The phenomenon also graphically illustrates the high level of substrate competition within the community, as soon as skeletal surfaces were laid bare, they were encrusted.

Compared to biohermal and biostromal complexes, patch reefs developed in carbonate-dominated lagoons there appear to show a slight increase in the proportion of complex skeletons relative to simple skeletons, but the data set is too small for a firm conclusion. Too few data of this type are available from other Devonian reefoid systems to invite comparisons.

## INTERGROWTHS

Intergrowths between stromatoporoids and other organisms have been recorded for over 150

TABLE 2. Percentage of acid insolubles, approximating percentage of siliciclastics for detrital sediment samples from selected facies of the Burdekin Formation.

| Facies/ interpreted environment | Specimen JCUR | % insoluble residue |
|---|---|---|
| Fossiliferous siltstone (adjacent to biostrome) | 34942 | 69.9 |
| | 34943 | 61.7 |
| | 34945 | 66.7 |
| Nodular limestone (adjacent to patch reefs) | 32113 | 20.7 |
| | 32164 | 20.2 |
| | 32180 | 9.7 |
| | 32181 | 11.1 |
| | 32183 | 12.5 |
| Silty floatstone or rudstone / nearshore biostromes (unsilicified detrital matrix) | 34950 | 10.1 |
| | 34951 | 18.2 |
| | 35003 | 19.1 |
| Floatstone / Biostrome (unsilicified detrital matrix) | 34957 | 8.3 |
| | 34955 | 11.0 |
| | 34965 | 7.5 |
| | 35001 | 10.1 |
| | 35002 | 4.2 |
| Framestone / Bioherm (unsilicified detrital matrix) | 32120 | 5.8 |
| | 32165 | 30.3 |
| | 32169 | 15.6 |
| | 32170 | 24.3 |

years following the erection of *Caunopora* by Phillips (1841). Tabulate corals allied to the syringoporids are, undoubtedly the most common organism found as stromatoporoid intergrowths, but rugose corals, algae, calcareous worm tubes and ?gastropods have been documented as intergrowths within stromatoporoid skeletons. Intergrowths with stromatoporoids from the Burdekin Formation mirror this overall pattern with tabulate corals abundant and rugose corals common. Enigmatic spiral tubes also occur but are more sporadic. Zhen & West (1997) noted intergrowths of symbiotic worms within *Salairella* sp. and *Litophyllum kominckí* and specimnes of *Helicosalpinx* sp. in *Hermatostroma* sp. from outcrops of the Burdekin Formation near Turtle Ck.

TABULATE CORALS. Earliest discussions of the caunopore state, the intergrowths of tabulate corals and stromatoporoids, date back to the introduction of *Caunopora placenta* of Phillips (1841). It was Roemer (1844), however, who first proposed caunopores to be the parasitic intergrowths of syringoporids and stromatoporoids. Subsequent to this early work, there has been much discussion of the caunopore state, the history of which was reviewed by Mistiaen (1984). This contribution outlined the various coral genera which have been attributed to the caunopore state, and reviewed the generic (stromatoporoid) and stratigraphic occurrences of such intergrowths. Tabulate corals intergrown with stromatoporoids have been assigned *inter alia* to *Syringopora* (e.g., Nicholson, 1886; Sleumer, 1969), *Syringoporinus* (e.g., Yavorsky, 1955, 1961) *Syringoporella* (e.g., Klovan, 1966; Birenheide, 1985) and *Caunopora* (Phillips, 1841; Birenheide, 1985).

Mistiaen (1984) reviewed the disparity between caunopore microstructure and that of *Syringopora*, casting doubt on the validity of assignment of caunopores to that genus. Subsequent authors have shown reluctance to refer caunopores to a tabulate genus, instead preferring *?Syringopora* (Kershaw, 1987) or *?Syringopora* cf. *vestita* Chudinova, 1971 (Young & Noble, 1989). An exception is Birenheide (1985) who assigned some caunopores to *Syringoporella*, and placed others within the portmanteau *Caunopora placenta* Phillips 1841. In line with Mistiaen's views, Birenheide also categorically stated that these caunopores are not *Syringopora*.

There are 2 types of stromatoporoid-tabulate coral intergrowths from the Burdekin Formation. Dominant are the regular intergrowths of a relatively small diameter, consistently-sized coral allied to *Syringoporella*? sp. (Fig. 13, A-D). Less common are the intergrowths of a slightly larger diameter tabulate coral more closely allied to *Syringopora* sp (Fig. 13 E-H.).

INTERGROWTHS OF *SYRINGOPORELLA?* SP. Such intergrowths are common and were found within the following taxa, in decreasing order of abundance; *Coenostroma wyatti*, *Stromatopora huepschii*, *Glyptostromoides hoiarschinovi*, and *Salairella* sp. These are all taxa with discontinuous thick coenosteles within a relatively irregular network. There are no occurrences of this type of syringoporid within stromatoporoids with a regular pillar-laminar structure. *Syringoporella*? sp. was not found outside stromatoporoid skeletons.

Individual corallites found as intergrowths within all these taxa are 0.45-0.75mm in diameter , and corallite walls are relatively thick (mean = 0.140mm, s= 0.027mm, n=60). Tabulae within the corallites are scarce, but are thin and slightly concave upwards. Some samples show unequivocal infundibuliform tabulae in addition to the slightly curved varieties. Data on corallite size and spacing (Fig. 14) show no significant variations between the different stromatoporoid taxa. It appears that syringoporid growth began in the early stages of the development of the

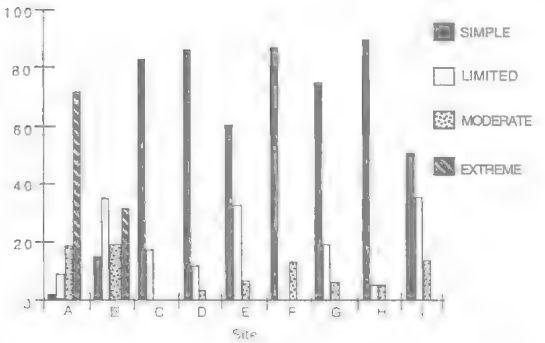



FIG. 12. Comparison of overgrowth occurrence in major stromatoporoid-bearing facies of the Burdekin Formation, showing percentages of simple skeletons, and those of limited, moderate and extreme complexity skeletons. A, fossiliferous siltstone facies, Fanning R., L788/16m n=63; B, fossiliferous siltstone facies, Fanning R., L788/22m n=26; C, biostromal facies, Fanning R., L788/60m n=24; D, biostromal facies, Fanning R., L788/75m n=29; E, dispersed stromatoporoid pavement, Horseshoe Bend, L787/ 200m n=16; F, patch reef, nodular limestone facies, Burdekin Downs, L781/ 25m n=15; G, grainy floatstone subfacies, Fletcherview, L778/25m n=48; H, framestone subfacies, Burdekin R., L781/30m n=200; I, *Endophyllum* siltstone facies, Fanning R., L788/ top of sequence n=14.

stromatoporoid colony, and its lateral development matched that of the host resulting in the distribution syringoporids throughout entire specimens of stromatoporoid. The syringoporid corallites are nearly always perpendicular to stromatoporoid coenostromes, unlike distributions illustrated by Young & Noble (1989: fig. 3a,b,d).

The corallites bud by the extension of stolons, approximately one third the diameter of the corallite, which arch gently upwards 1 or 2 stromatoporoid laminae distant from their origin. Surrounding each syringoporid corallite is a thin sheath of stromatoporoid skeletal material, up to 0.2mm thick and coenostromes upwardly inflect where they meet the corallite wall.

Data on the tangential distribution of individual corallites was collected by measuring 'nearest neighbours'. In each thin section individual corallites were selected and the distances to the nearest 4 corallites was measured. These data show little variation in the spacing between adjacent corallites; in tangential section the syringoporids are extremely regular in their distribution across the stromatoporoid colony (Fig. 13A,D).

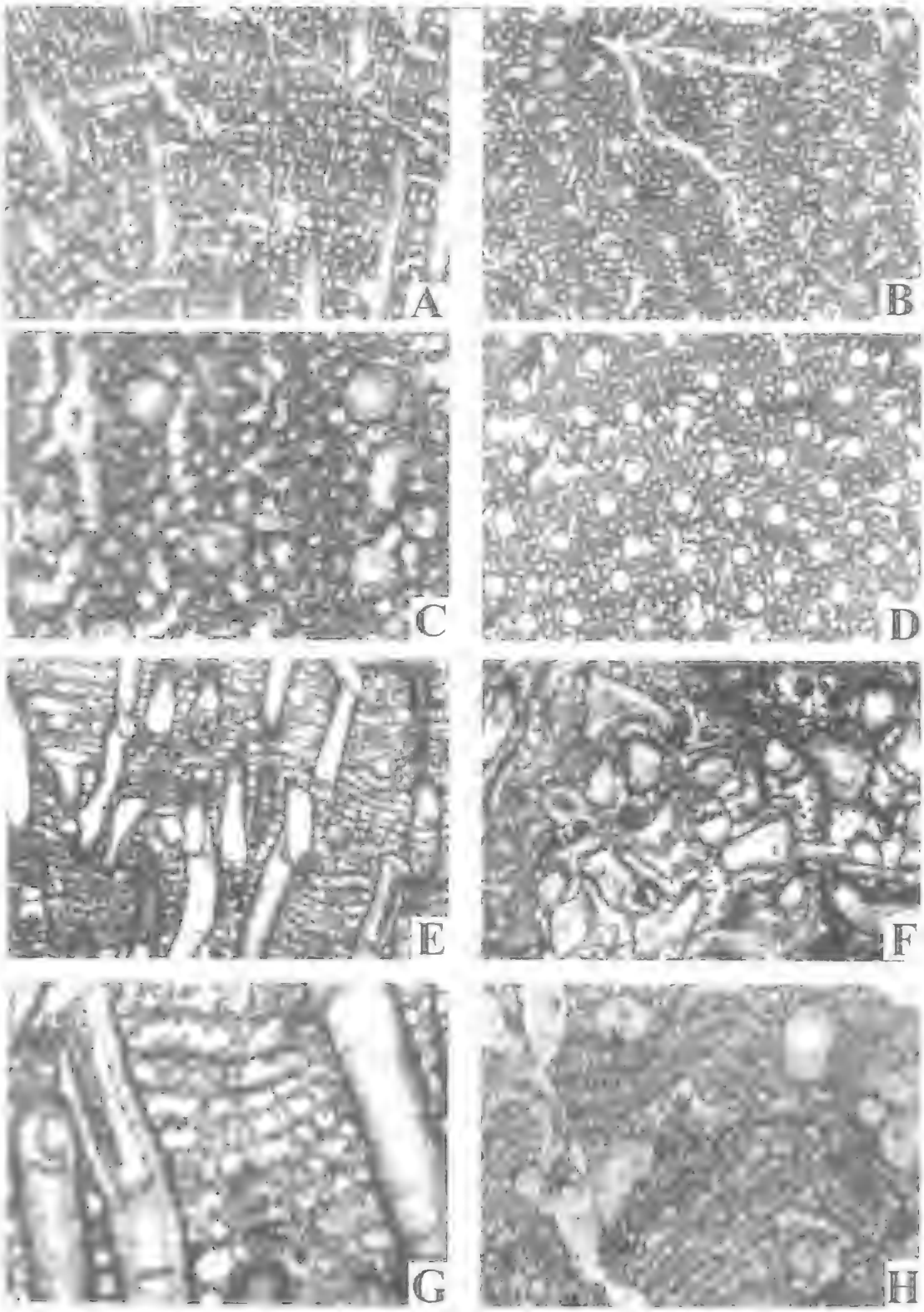
DISCUSSION. Young & Noble (1989) suggested that syringoporid growth within stromatoporoid skeletons was constrained by skeletal density of the host. All the taxa with *Syringoporella*? sp. intergrowths have comparable skeletal density, and possess a moderately irregular skeletal architecture. Host selection of stromatoporoids by corals was suggested by Kershaw (1987) who observed that ?*Syringopora* sp. occurred in only one taxon of stromatoporoid from Hemse, Gotland, Sweden. Unlike the present study, Kershaw's intergrowths were described from a host taxon with a regular pillar-laminar skeletal grid.

Young & Noble (1989) considered that the living syringoporid polyp was maintained at or just above the stromatoporoid growth surface. If the latter were true, then part of the side of the coral skeleton would be exposed to algal micritisation. Given that there are no micrite rims on the corallites, they must have been maintained at the same growth level as the stromatoporoid soft tissue surface. Upward inflection of stolons reflect the need to maintain upward growth with the growth of the stromatoporoid.

The secretion of stromatoporoid skeleton around the corallites suggests a response to the syringoporids presence by the stromatoporoid soft tissue and may suggest an advantage of structural support being afforded the coral. It also suggests likely soft-part contact, given the interpreted level growth surface for both organisms.

Regular growth would suggest a mutualistic rather than a detrimentally parasitic relationship. Coral preference for stromatoporoids of a particular skeletal style would support a non-infestation relationship. The equivalence of growth surface for both organisms suggests there was no additional substrate advantage for the coral over the stromatoporoid. Kershaw (1987) noted that syringoporid intergrowths from the Silurian of Gotland were most common in high-energy, shallow water facies. In the Burdekin Formation *Syringoporella*? sp. intergrowths are most common in distal shelf facies, but this is most probably due to the preference of host taxa for these environments.

Whether the relationship between the stromatoporoids and corals was one of mutualism, commensalism or parasitism will remain unresolved until preserved soft parts are discovered. Nevertheless parasitism is rejected given the lack of detrimental effect on the stromatoporoid.


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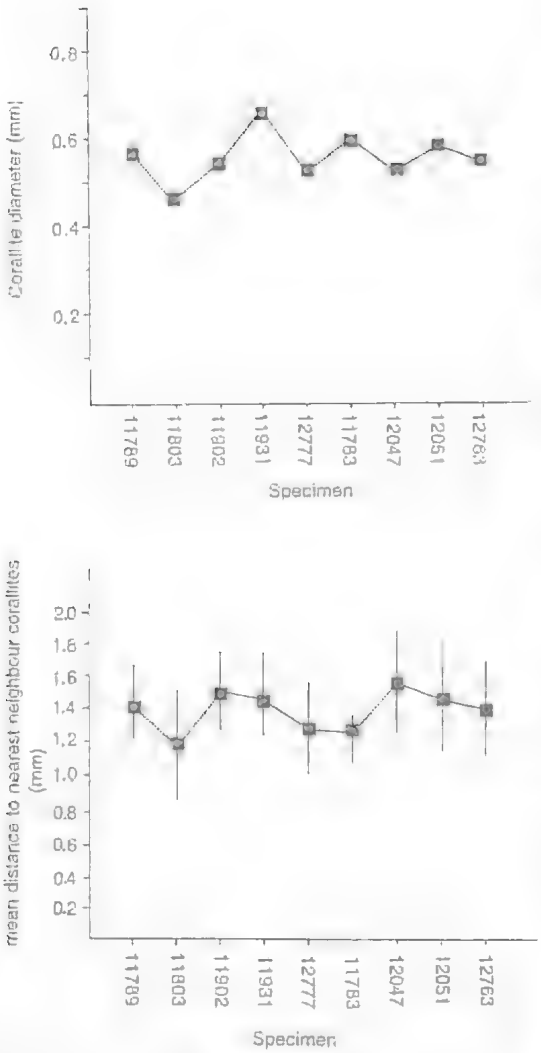



FIG. 14. Corallite diameter and spacing for intergrowths of *Syringoporella*? sp. n=30 for each specimen.

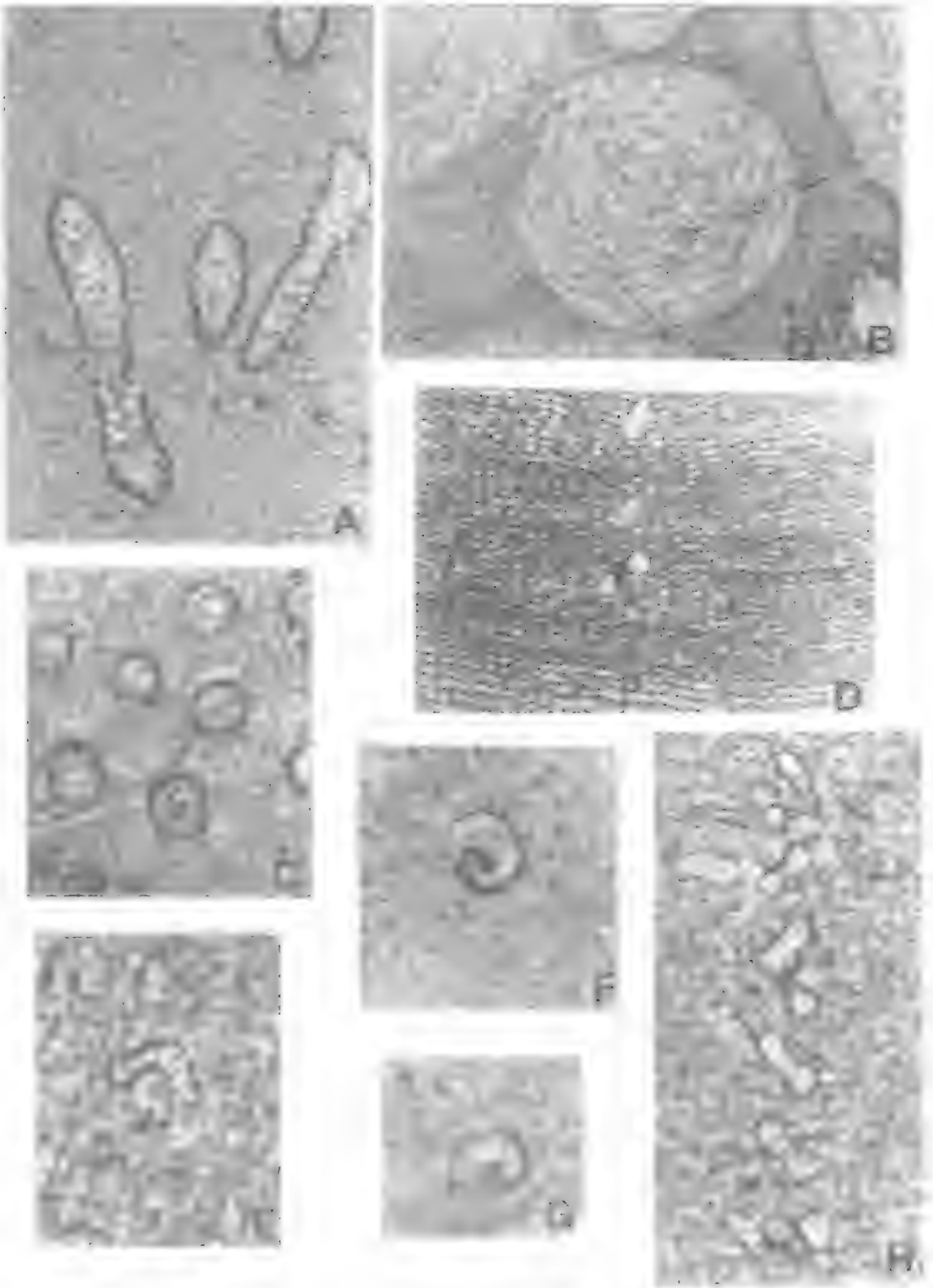
Problems with the affinity of the caunopore organism have been raised by Mistiaen (1984) based on studies of ultra-thin microstructure of the corallite wall. Kershaw (1987) noted significantly different microstructures in caunopores than those of Mistiaen (1984) and most authors (e.g., Kershaw, 1987; Young & Noble, 1989) note that intergrowth syringoporids differ from those coexistent outside stromatoporoid skeletons. It is likely, given the relationship of syringoporid skeletal material within stromatoporoids, that both macro and microstructural modification took place.

The second variety of stromatoporoid-tabulate coral intergrowth is less common. The corallites are larger than *Syringoporella*? sp., have definite infundibuliform tabulae, thinner corallite walls and are not as regularly distributed in the host. These are known from *Hermatostroma episcopale* and *Gerronostroma* sp. Growth initiated near the base of the skeleton but was not regular or consistently oriented throughout the skeleton. The taxonomic affinities of this form are uncertain, but its gross morphology invites comparison with *Syringopora*.

RUGOSE CORALS. A number of taxa, including *Gerronostroma* sp., *Stromatopora* sp., *Hermatostroma maculatum* and *Gerronostroma hendersoni* contain sporadic rugose coral intergrowths, including *Disphyllum* sp., *Stringophyllum* sp. and other unidentified rugose coral taxa (Fig. 15A-D). They mostly occur as isolated corals within the stromatoporoid skeleton, but a few stromatoporoids contain moderate numbers of rugose corals. They are not regularly distributed throughout the skeleton, often have a dark micritic line at the edge of the coral, and the stromatoporoid laminae inflect upwards against the coral wall in vertical section and the skeletal structure wraps aroundFig. 14. Corallite diameter and spacing for intergrowths of *Syringoporella*? sp. n=30 for each specimen. the coral. Coral growth is commonly oblique to stromatoporoid growth layers. The presence of the marginal micrite envelope suggests that the rugose coral grew at a level above the stromatoporoid surface, thus enabling endolithic algae to infest the exposed corallite skeleton. In this way the coral is exploiting the stromatoporoid skeleton as substrate and for structural support. The random growth orientations suggest fortuitous rather than deliberate intergrowth.

OTHER ORGANISMS. Helical-spired tubes allied with *Helicosalpinx* sp. are sporadic within

FIG. 13. Tabulate coral intergrowths with stromatoporoids from the Burdekin Formation. A-D, intergrowths of ?*Syringoporella* sp. with *Coenostroma wyatti* sp. nov. A-C, F12763. A, vertical section, × 5; B, tangential section, × 5; C, tangential section, × 15; D, F11783, tangential section, × 5. E-H, intergrowths of *Syringopora* sp. E-F, F12678, *Gerronostroma* sp.; F, vertical section, × 5; E, tangential section, × 5; F, vertical section, × 15; H, F11870, *Hermatostroma episcopale* Nicholson, tangential section, × 5.


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many stromatoporoid taxa (Fig. 15 E-H) and the massive tabulate coral *Alveolites* sp. cf. *A. intermixtus*. These are found most commonly within specimens of *Actinostroma filitextum*, *Gerronostroma hendersoni* and *Gerronostroma* sp. Such tubes have been allied to the Vermes (Plusquellec, 1968a,b; Oekentorp, 1969), and possibly gastropods (Cockbain, 1984). Some have thin partitions (Fig. 15) confirming that the organism sealed its living chamber. Such partitions led Cockbain (1984) to suggest septate gastropods were possibly inquilinistic in habit. Zhen & West (1997) concluded that a live-live interaction took place between unnamed worms and *Salairella* and *Litophyllum*.

## STROMATOPOROID AND OTHER COMMUNITIES OF THE FANNING RIVER GROUP

One of the fundamental aims of this work is to discuss the association of faunal elements in relation to the various interpreted environments of the Fanning R. Group. I have not dealt in detail with the rugose corals, save cursory identifications following Zhen (1991) who described a number of rugose coral associations for the group. Rigorous taxonomic attention has not been given to the large tabulate coral fauna; rather open nomenclature identifications suffice for this study. The stromatoporoid composition of each fauna is variably dependant on the quality of preservation which greatly determines the identifiablity of individual stromatoporoid specimens. Of the approximately 1000 specimens of stromatoporoids collected, slightly less than one half were identifiable in thin section. Some areas, especially Kirkland Downs and Mount Podge, contained stromatoporoid faunas that were unidentifiable due to diagenesis.

The taxa described below and key additional taxa are tabulated relative to facies groupings (Table 3). On the basis of this, 10 communities are recognised for the Group based on the stromatoporoid-tabulate coral-and molluscan faunas: 1) *Burdikinia*; 2)*Modiomorpha*; 3) *Stachyodes-Syringopora*; 4) *Clathrocoilona spissa -Aulopora*; 5)*Ferestromatopora heideckeri-Amphipora ramosa-Stringocephalus*; 6) *Hermatostroma maculatum-Gerronostroma hendersoni*; 7) *Coenostroma-Hermatostroma episcopale*; 8) *Amphipora pervesiculata*; 9) *Endophyllum* community; and, 10) cephalopod association (not in situ).

## GUILD STRUCTURE

Fagerstrom (1987) demonstrated the general utility of the guild concept to reefs, both modern and ancient. He defined 5 major guilds within the reefal environment; constructor, binder (encruster), baffler, dweller and destroyer, in order to account for the spatial and resource organisation of reefs. The constructor guild is the most important to the reefal ecosystem, its 'vigorous expression' being a necessary condition for reefal community development (Fagerstrom, 1987:203). Whereas this guild concept is readily applied to reefs (sensu framestone-type bioherms), problems in the role and definition of guild states arise when the concept is applied to biostromal deposits which, according to Fagerstrom (1987), are not true reefs. Clearly most of the general concept of reefal guilds can be transferred to biostromal communities, but the biostromal guild structure differs in the role of binders or encrusters, and the equivalent of the topographic relief-producing constructor guild. Although the organisms are similar, and in some cases involving identical taxa, the organisms are commonly isolated, or only partially bound to their neighbours. Therefore the use of 'constructor', in the sense of building a reef with topographic relief, is somewhat of a misnomer when applied to biostromes. Fagerstrom's (1987) binder (encruster) guild included organisms which encrusted other organisms and the sediment, thus binding the reef framework together. In biostromes the encrustation of larger organisms and the binding of sedimentary substrate are often performed by different organisms. For instance it is difficult to reconcile placing auloporid corals encrusting a larger skeleton in the encruster guild with laminar stromatoporoids which cover a surface of muddy

FIG. 15. A-C, rugose coral intergrowths with stromatoporoids from the Burdekin Formation. A, F11892, *Gerronostroma* sp. with rugose corals, × 5; B, F12016, *Gerronostroma* sp. with rugose corals, × 6; C, F11892, tangential section, × 5. D-H, 'vermetid' intergrowths within stromatoporoids from the Burdekin Formation. D, F11939, *Actinostroma filitextum* Lecompte, 1951, vertical section, × 6; E, F11892, *Gerronostroma* sp. with partitioned commensal, vertical section, commensal is oriented obliquely, × 15; F, F11936, *Actinostroma filitextum* Lecompte, 1951, tangential section, × 20; G, F11879, *Actinostroma filitextum* Lecompte, 1951, tangential section, × 20; H, F11892, *Gerronostroma* sp., vertical section, × 15.

| Taxa \ Facies of Cook (1995) | abraded bioclast coarse siliciclastic | fossiliferous sandstone | fossiliferous siltstone | biostrome in fossiliferous siltstone | nodular limestone | patch reefs in nodular limestone | coverstone | bio-hermal facies | stromatoporoid biostromal facies | dispersed stromatoporoid packstone | coralline packstone | *Endophyllum* siltstone | micritic carbonate |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *Actinostroma filitextum* | | | | | | | | ● | | | | | |
| 2. *Aculatostroma?* sp. | | | | | | | | | | | ○ | | |
| 3. *Clathrodictyon* sp. | | | | | | | | ○ | | | | | |
| 4. *Atelodictyon fallax* | | | | ? | | | | ● | ● | | | | |
| 5. *Schistodictyon* sp. | | | | | | ○ | | | | | | | |
| 6. *Gerronostroma hendersoni* | | | | ? | ○ | ● | ● | ● | ○ | | ● | | |
| 7. *Gerronostroma* sp | | | | ● | | | | ● | ● | | | | |
| 8. *Anostylostroma ponderosum* | | | | | | | | ● | | | | | |
| 9. *Anostylostroma* sp. | | | | | | | | | ● | | | | |
| 10. Gen. Et sp. indet cf. *Clathrodictyella* | | | | | | | | ○ | | | | | |
| 11. *Stictostroma* sp. | | | | | | | | | | ○ | | | |
| 12. *Clathrocoilona abeona* | | | | | | ● | | ● | | | ● | | |
| 13. *Clathrocoilona spissa* | | | | ● | | | | | | | | ● | |
| 14. *Hermatostroma episcopale* | | | | | | | | ○ | ○ | ● | ● | | |
| 16. *Hermatostroma maculatum* | | | | | | ● | ● | ● | ● | | | | |
| 16. *Trupetostroma zheni* | | | ● | | ● | | | | | | | | |
| 17. *Stachyodes crassa* | | | | | ○ | | | | | | | | |
| 18. *Stachyodes costulata* | ○ | ○ | ● | | ● | ● | ● | ● | ■ | ○ | ○ | | |
| 19. *Stachyodes* sp. A | | | | | | | | | | | ○ | | |
| 20. *Stachyodes* sp. B | | | | | | | | | | ○ | | | |
| 21. *Amphipora ramosa* | | | | | | | | | ● | | | | |
| 22. *Amphipora pervesiculata* | | | | | | | | | | ■ | ● | | |
| 23. *Eurymphipora merlini* | | | | | | | ● | ○ | | ○ | ● | | |
| 24. *Stromatopora huepschii* | | | | | | ● | | | ● | ● | ● | ● | |
| 25. *Stromatopora* sp. | | | | ● | | | | | ● | | | | |
| 26. *Pseudotrupetostoma ambiguum* | | | | | | | | | ○ | | | | |
| 27. *Ferestromatopora heidecker* | | | | ● | | | | | ■ | ● | | | |
| 28. *Salairella buecheliensis* | | | | | | | | ● | | ● | ● | ● | |
| 29. *Salairella S. cooperi* | | | | | | | | | ● | | | | |
| 30. *Salairella* sp | | | | | | | | | | | ● | | |
| 31. *Glyptostromides boiarschinovi* | | | | | | | | | | ● | ● | | |
| 32. *Taleastroma* sp | | | | | | | | | ○ | | | | |
| 33. *Coenostroma burdekinense* | | | | | | | | ○ | | ● | ● | | |
| 34. *Coenostroma wyatti* | | | | | | | | | | ● | ● | | |
| 35. *Parallelopora?* Sp. | | | | | | | ● | ● | | | | | |
| MOLLUSCS | | | | | | | | | | | | | |
| *Burdikinia burdekinensis* | ● | ● | ○ | | | | | | | | | | |
| *Amphelissa carinatum* | ● | ● | ○ | | | | | | | | | | |
| *Labrocuspis nodosa* | ● | ● | ○ | | | | | | | | | | |
| *Fletcherviewia septata* | | ● | | | | | | | | | | | |
| *Modiomorpha mitchellae* | | | ■ | | | | | | | | | | |
| *Phenacocyclas pohli* | | | | | | | | ● | | | | | |
| *Tanaodon louderbacki* | ● | ● | | | | | | | | | | | |
| TABULATE CORALS | | | | | | | | | | | | | |
| *Heliolites* sp | | | ● | | | | ● | ● | ● | ● | ● | ● | |
| *Cladopora* sp. | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | ○ |
| *Alveolites* sp. | ○ | ○ | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | |
| *Aulopora* sp. (laminar) | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | |
| *Syringopora* sp | | | ● | ● | ● | | ● | ● | ● | ● | | ● | |
| *Romingera* sp. | | | ● | ● | ● | | ● | | | | | | |
| *Thamnopora* sp | ○ | ○ | ● | ● | ● | | | | | | | ● | |
| *Litophyllum kaninchi* (Chaetetid) | | | | | ● | ● | ● | ● | ● | ● | ● | ● | |
| Brachiopods (general) | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | |
| atrypids | | | ● | | | | | | ● | ● | ● | ● | ○ |
| *Stringocephalus* sp | | | | | | | | | ● | | | | |

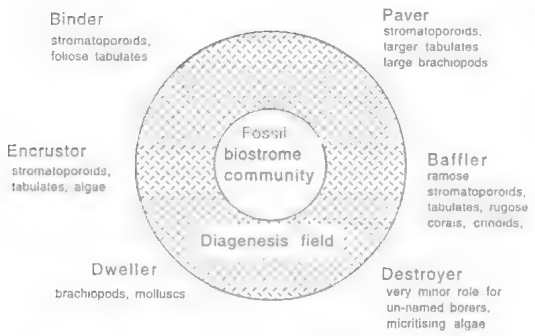



FIG. 16. Potential guild structure for Middle Devonian biostromes of the Burdekin Formation, modified from the reefal guild structure of Fagerstrom (1987).

carbonate sediment. Hence it is proposed, that in discussing the guild structure of level bottom biostromes (as opposed to bioherms) the guild group 'paver' be recognised to describe large constructor-equivalent organisms, and that 'binders' be recognised as the sediment coverers as distinct from the 'encrusters' of large skeletons. Bafflers, dwellers and destroyers remain herein as defined by Fagerstrom (1987). Thus the potential guild structure of the biostrome is given below (Fig. 16). The guild membership is listed for each community, as appropriate, below.

*BURDIKINIA* COMMUNITY. *The Burdikinia* community is a mollusc-dominated fauna which occurs within abraded bioclast coarse siliciclastic facies, fossiliferous sandstone facies and impure limestone facies, generally at the base of the Fanning R. Group, and within clastic intercalations throughout the carbonate sequence. The assemblage thrived on the coarse clastic, often turbulent, shoreface and in shallow inner shelf environments.

Four molluscan taxa dominate the assemblage; the gastropods *Burdikinia burdekinensis* (Etheridge, 1917), *Amphelissa carinatum* (Heidecker, 1959), *Labrocuspis nodosa* Heidecker and the bivalve *Tanaodon louderbacki* Kirk, 1927. In addition there is a fourth rarer gastropod *Fletcherviewia septata* Cook, 1993, scattered tabulate corals, the common rugose coral *Temnophyllum* sp. and sporadic *Stachyodes costulata* Lecompte complete the assemblage. At Fletcherview L778, characteristic trace fossils (see Cook, 1993a) provide a useful insight into the molluscan assemblage.

The mobile sandy substrate would have been a habitat particularly attractive to the gastropods. Algal grazing would have been restricted in the more offshore coralline-stromatoporoid banks where available non-muddy substrate was occupied by stromatoporoids and coralline forms. Mud-dominant lagoons would have provided additional problems due to the large size (hence weight) of the shells. Because the gastropods were thick-shelled and fairly heavy, they were well suited to this high energy environment. There were 2 main strategies for dealing with turbulent conditions on the habitat. All 4 gastropods are heavy forms, but *Burdikinia, Labrocuspis and Amphelissa* are all compact, relatively low-spired, robust forms. *Labrocuspis* has been interpreted by Kase (1989) to have 2 modes of life; creeping over the substrate and partly infaunal. This second partly buried life mode may have been a strategy for dealing with high turbulence conditions.

*MODIOMORPHA* COMMUNITY. This community could be considered a variant of the *Burdikinia* community, as many of the elements are common to both. It occurs in the much abbreviated representation of Burdekin Formation near Boundary Ck, Paynes Lagoon Station and consists of in situ conjoined *Modiomorpha mitchellae* Cook, with minor *Burdikinia*, *Labrocuspis*, *Thamnopora* sp, and rare rugose corals. Modiomorphs are partly infaunal epibyssate suspension feeders with the gape protruding from the substrate (Bailey, 1983). The community is dominated by the modiomorph with subordinate coral bafflers.

*STACHYODES-SYRINGOPORA* COMMUNITY (Table 4). Baffler guild organisms overwhelmingly dominate this community which is largely exclusive to soft, muddy-bottomed, innershelf, impure bays and lagoons. The role of pavers on the lagoon floor in this impure environment was limited. Patch reefs developed as small 'rauks' or low biohermal accumulations within these bays and are not included in this community. *Stachyodes costulata* is the ubiquitous faunal element, the robustly dendroid tabulate *Thamnopora* sp. is abundant. Solitary rugose corals are generally of the '*Charactophyllum* sp.' type, showing the low,

TABLE 3. Distribution of stromatoporoid and other key taxa within facies of the Big Bend Arkose and Burdekin Formation. 1. Occurs as encrusting fauna and within boulder interstices. ○ - rare, ● - common.

TABLE 4. Faunal components and guild status, of the *Stachyodes- Syringopora* community, with dominant forms in bold.

| Bafflers | Pavers | Encrusters | Dwellers |
|---|---|---|---|
| ***Stachyodes costulata*** | *Litophyllum koninckii* | *Stachyodes costulata* | ***Charactophyllum*** sp. |
| ***Syringopora* sp.** | *Gerronostroma hendersoni* | *Aulopora* sp. | *Pseudomicroplasma* sp. |
| **alveolitids** | | | *Disphyllum* sp. |
| *Stachyodes crassa* | | | bivalves |
| *Trupetostroma zheni* | | | brachiopods |
| *Romingeria* sp. | | | ?algae |
| branching alveolitid | | | |

cup-shaped form better suited to muddy substrate and sediment expulsion as discussed by Zhen (1991). Another common rugose coral is *Pseudomicroplasma australe* (fide Zhen, 1991). Two very common tabulate coral elements are *Romingeria* and *Syringopora*. Both had a bushy rather than encrusting growth strategy within the impure inner shelf. This community is dominated by bushy forms capable of gaining height above the muddy, substrate. Abundant molluscan hash associated with this community suggests a large population of small, as yet, unidentified bivalves.

At 2 localities members of this community are found in facies representing preserved headlands. Common encrusting *Alveolites* sp. and *Stachyodes costulata* are found as interstitial fauna, and show negligible transport. These elements adopted an encrusting and interstitial strategy to enable them to exploit the barely subtidal rocky headlands. It appears that this fauna was restricted by substrate relief to where turbulence and sedimentation rate were enhanced, and the substrate too mobile to allow larval settling and growth. However *Stachyodes costulata* and *Alveolites* sp. are found as part of a rare fauna within facies interpreted as marine headlands where both are found as unabraded branches. *Stachyodes costulata* is also found encrusting granite boulders and cobbles. This relationship is interpreted to represent encrustation of boulder interstices, which afforded some protection in a high energy environment. Within reefoid environments elements of this community were reduced to interstitial, subsidiary roles, and the decrease in importance of *Stachyodes* and *Thamnopora* sp. was progressive across the shelf. Seaward of the biohermal complex, this community was not able to compete with that dominated by the more delicate *Amphipora* and *Cladopora*. The taxa of this community clearly were more successful on the muddier substrates due to their ability to grow above the seafloor. By inference it may have been more tolerant of siliciclastic input than other dendroid forms found within more offshore facies.

## *CLATHROCOILONA SPISSA-AULOPORA* COMMUNITY (Table 5).

This community is best known from the Fanning River area and is dominated by encrusters and bafflers. It is perhaps the most unusual of the stromatoporoid assemblages in the Fanning River Group. It inhabited low, loose biostromes and pavement biostromes located within the impure muddy bays and lagoons of the innermost shelf representing environments dominated by fine-grained siliciclastics A large majority of skeletons within this environment are compound, containing overgrowths of a number of tabulate, stromatoporoid, rugose coral and algal taxa. The skeletal growth form is variable and irregular in profile but ranges in overall shape from laminar to bulbous, as previously discussed. Encrusters gained purchase on small coral or stromatoporoid fragments and skeletons developed as a series of overgrowths. Baffler elements are dominated by alveolitid corals including *Thamnopora* sp., rugose corals including *Disphyllum* sp., *Grypophyllum* sp, and minor *Stachyodes costulata*. Community composition reported below was biased by the general poor state of preservation of stromatoporoids in facies containing this community. Pervasive neomorphism and silicification has rendered many specimens unidentifiable. It is likely that *C. spissa* dominated the innermost shelf due its

TABLE 5. Members of *Clathrocoilona spissa- Aulopora* community and their proposed guild designations. Dominant taxa shown in bold.

| Encrusters | Pavers | Bafflers | Dwellers |
|---|---|---|---|
| ***Clathrocoilona spissa*** | *Stromatopora* sp. | ***Thamnopora* sp.** | *Syringopora* sp. |
| *Stromatopora* sp. | *Gerronostroma* sp. | *Cladopora* sp. | rugose corals |
| *Ferestromatopora heidecker*i | *Stachyodes costulata* | *Stachyodes costulata* | gastropods |
| *Gerronostroma* sp. | unidentifiable | | bivalves |
| ***Aulopora* spp.** | stromatoporoid | | brachiopods |
| *Litophyllum koninckii* | *Heliolites* sp. | | |
| algae | | | |
| encrusting alveolitid | | | |

TABLE 6. Members of *Ferestomatopora heideckeri- Amphipora ramosa-Stringocephalus* community and their proposed guild designations. Dominant taxa shown in bold.

| Pavers | Baffiers | Encrusters | Dwellers |
|---|---|---|---|
| ***Ferestromatopora heideckeri*** | ***Amphipora ramosa*** | *Clathrocoilona spissa* | other rugose corals |
| *Atelodictyon fallax* | *Cladopora* sp. | *Stromatopora* sp. | brachiopods |
| *Gerronostroma* sp. | ***Dendrostella trigemme*** | *Alveolites* sp. | ***Stringocephalus* sp.** |
| *Stromatopora* sp. | *Cladopora* sp. | *Aulopora* sp. | molluscs |
| *Salairella* cf. *S cooperi.* | *Thamnopora* sp. | | |
| *Gerronostroma hendersoni* | *Stachyodes costulata* | | |
| *Litophyllum koninckii* | | | |
| *Heliolites* sp. | | | |

greater ability to rapidly encrust exposed skeletal surface and was slightly better tolerance of fine-grained siliciclastic input and its associated effects. *Aulopora* abundance was controlled by hard substrate availability.

*FERESTROMATOPORA HEIDECKERI-AMPHIPORA RAMOSA-STRINGOCEPHALUS* COMMUNITY (Table 6). This community dominates the biostromal complex, and is best known in the Fanning River area. It inhabited a wide zone ranging from nearshore to carbonate-dominant proximal shelf within extensive biostromal banks of very low relief. The substrate was highly variable, ranging from micritic muds to rubble with dendroid forms better preserved on, and presumably having preferred, the muddier substrates. The community is dominated by low to medium domical forms, and an abundance of delicate dendroid faunal elements. The large brachiopod *Stringocephalus* sp. is a common component, sporadically so abundant as to dominate local biostrome faunas. Given their large size, abundance and concentration into clumps they are probably a rare example of brachiopod which could be considered as a paver guild member. The composition of this fossil community varies both laterally and vertically, and is best expressed within the carbonate dominated, proximal shelf facies. Occurrences of the community lower in the sequence are largely lacking in *Stringocephalus*, the first occurrence of this brachiopod being 27m above the base of the sequence within the type section. Lower occurrences also commonly show reduced numbers of *Amphipora*, the taxon being replaced by higher numbers of *Stachyodes costulata*. Biostromal units occur to the north of Fanning River (L789), where stromatoporoids and corals numbers are significantly reduced and large concentrations of *Stringocephalus* sp. dominate.

The community is clearly dominated by the baffler and paver guilds. Stromatoporoids and other pavers are closely spaced within patchy zones, with the abundant baffler and dweller fauna interstitial and between patches. The encruster guild is less dominant within this community. Taxa which in other communities are important encrusters are more prevalent as pavers within this biostromal environment. Preservationally this community is affected by common obliterative neomorphism and silicification rendering many stromatoporoid skeletons unidentifiable. This situation is particularly true for fauna within the stromatoporoid biostromal facies at Kirkland Downs area where neomorphism and dolomitisation have rendered

TABLE 7. Major faunal components of the *Gerronostroma hendersoni- Hermatostroma maculatum* community and their guild memberships, with dominant forms in bold.

| Constructors | Encrusters (Pavers) | Baffiers | Dwellers |
|---|---|---|---|
| ***Gerronostroma hendersoni*** | *Clathrocoilona abeona* | ***Stachyodes costulata*** | ***Heliolites* sp.** |
| ***Hermatostroma maculatum*** | *Euryamphipora merlini* | *Thamnopora* sp. | *Alveolites* sp. |
| *Actinostroma filitextum* | *Aulopora* sp. | *Cladopora* sp. | numerous rugose corals |
| *Atelodictyon fallax* | *Alveolites* sp. | *Stringophyllum* spp. | *Litophyllum koninckii* |
| *Stromatopora huepschii* | (*Gerronostroma hendersoni*) | *Alveolites* sp. | brachiopods |
| *Salairella bucheliensis* | (*Hermatostroma maculatum*) | Gen. et sp. indet cf. | molluscs |
| *Coenostroma wyatti* | | *Clathrodictyella* | *Romingeria* sp. |
| *Anostylostroma ponderosum* | | | *Syringopora* sp. |
| *Parallelopora?* sp. | | | |
| *Clathrodictyon* sp. | | | |

TABLE 8. Faunal components of the *Coenostroma- Hermatostroma episcopale* community and their guild designations, with dominant components in bold.

| Pavers | Encrusters | Bafflers | Dwellers |
|---|---|---|---|
| ***Hermatostroma episcopale*** | *Aulopora* sp. | *Amphipora pervesiculata* | *Heliolites* sp. |
| ***Coenostroma burdekinense*** | *Alveolites* sp. | *Cladopora* sp. | atrypids |
| ***Coenostroma wyatti*** | *Clathrocoilona abeona* | *Alveolites* sp. | other brachiopods |
| *Salairella bucheliensis* | *Euryamphipora merlini* | *Aphyllum* sp. | *Syringopora* sp. |
| *Stromatopora huepschii* | | *Stringophyllum* sp. | molluscs |
| *Glyptostromoides boiarschinovi* | | *Stachyodes costulata* | *Romingeria* sp. |
| *Stromatopora* sp. | | *Stachyodes* sp. A | other rugose corals |
| *Parallelopora* sp. | | *Stachyodes* sp. B | |
| *Salairella* sp. | | | |
| *Stictostroma* sp. | | | |
| *Aculatostroma* sp. | | | |
| *Litophyllum koninckii* | | | |

most stromatoporoids unidentifiable to species level. Present at this locality are the stromatoporoids; *Amphipora ramosa, Stromatopora* cf. *S. huepschii* (with caunopores), *Hermatostroma* cf. *H. maculatum*, *H. episcopale*, *Stromatopora* sp. and a number of unidentifiable taxa; tabulate corals *Heliolites* sp., *Syringopora* sp., large *Alveolites* sp., fasciculate *Alveolites* sp., *Cladopora* sp. and the chaetetid *Litophyllum koninckii*. Additionally there are a large number of colonial rugose corals, particularly *Taimyrophyllum* spp. (Zhen, 1991). The biostromal fauna at Kirkland Downs is tentatively assigned to this community.

*GERRONOSTROMA HENDERSONI-HERMATOSTROMA MACULATUM* COMMUNITY (Table 7). This community was the main reef-occupying faunal assemblage. It is found within patch reefs of the nodular limestone facies, laminar stromatoporoid pavements of the coverstone facies, and the biohermal complex including primary reefal framestone and grainy floatstone representing inter-reef channel. The 2 constructors are *G. hendersoni* and *H. maculatum*. There are no non-stromatoporoid constructor guild members within the reefal complex. Large tabulate corals are a subsidiary component of the reefal community, and do not form part of the essential reefal framework. There is moderate diversity in the baffler and dweller guilds, with an abundant rugose coral and fasciculate tabulate coral fauna. Guild overlap is demonstrated by the main elements of the fauna. Within the laminar stromatoporoid pavement *G. hendersoni, H. maculatum,* and less commonly *Parallelopora*? sp. should be regarded as paver guild members.

This community was restricted seaward by depth, and leeward by siliciclastics, represented either by moderate input of fine siliciclastics or by coarse siliciclastic mobile substrates. The community could survive within the muddy carbonate lagoon where substrate was available and when sedimentation rate permitted.

*COENOSTROMA-HERMATOSTROMA EPISCOPALE* COMMUNITY (Table 8). This community is found within the dispersed stromatoporoid pavements and coral thickets of the dispersed stromatoporoid packstone facies, overlapping to the coralline packstone facies best characterised by the *Amphipora pervesiculata* community described below. It is dominated by baffler guild members, with a significant representatives of paver guild members. It is restricted seaward by depth, and landward by the biostromal and biohermal zones. Given that some elements of this fauna are found in the biohermal and biostromal facies as part of other

TABLE 9. Faunal components of the *Amphipora pervesiculata* community and their interpreted guild memberships, with dominant taxa in bold.

| Pavers | Encrusters | Bafflers | Dwellers |
|---|---|---|---|
| *Hermatostroma episcopale* | *Aulopora* sp. | ***Amphipora pervesiculata*** | brachiopods |
| *Salairella bucheliensis* | *Alveolites* sp. | ***Cladopora* sp.** | molluscs |
| *Stromatopora huepschii* | *Syringopora* sp. | ***Alveolites* sp.** | rugose corals |
| *Coenostroma burdekinense* | *Euryamphipora merlini* | *Aphyllum* sp. | *Syringopora* sp. |
| *Coenostroma wyatti* | | *Stringophyllum* sp. | gastropods |
| *Heliolites* sp. | | rare *Stachyodes* spp. | |

communities, it appears that they could not compete effectively with other taxa in such communities. Sedimentation rate was probably too high in the biohermal and biostromal facies with siliciclastic input at the limits of tolerance for the main elements of the *Coenostroma-Hermatostroma episcopale* community.

TABLE 10. Members of the *Endophyllum* community and their guild designations with dominant forms in bold.

| Constructors | Encrusters | Bafflers | Dwellers |
|---|---|---|---|
| ***Endophyllum* sp.** | *Clathrocoilona spissa* | *Alveolites* sp. | atrypids |
| rare sponges | *Stromatopora huepschii* | *Cladopora* sp. | other brachiopods |
| larger alveolitids | *Salairella bucheliensis* | *Dohmophyllum* sp. | other rugose corals |
| ***Heliolites* sp.** | *Aulopora* sp. | *Stringophyllum* sp. | |
| *Litophyllum koninckii* | *Alveolites* sp. | | |
| *Alveolites* sp. | *Litophyllum koninckii* | | |

*AMPHIPORA PERVESICULATA* COMMUNITY (Table 9). Delicate *Amphipora* dominated this community, living within thickets of the coralline packstone and dispersed stromatoporoid packstone facies. Larger skeletal members of the community, particularly stromatoporoids and heliolitids, are minor faunal components. There is a high proportion of thinly branched stromatoporoids, tabulate corals and long-branched rugose corals. The community extended from the seaward edge of the bioherm and biostromal complex, well across the shallow distal shelf. Where there was limited biohermal or biostromal development, the community extended across the entire carbonate-dominant shallow shelf. *Amphipora* has been traditionally regarded as a lagoonal faunal component (Noble, 1970), however, the presence of *A. pervesiculata* in a number of different, if adjacent, facies, suggests that the genus may have been more widely distibuted through the available niches. Toppling and reorientation of the many delicately branched skeletons suggest an ambient environment with gentle current activity.

Isolated colonies of *Syringopora* sp and *Aulopora* sp. are common to the community. These are regarded as 'pioneers', often inhabiting substrates and areas seemingly unsuited to other groups.

*ENDOPHYLLUM* COMMUNITY (Table 10). This community is restricted to the *Endophyllum* siltstone facies, and is dominated by the large colonial rugose coral. The role of stromatoporoids is much reduced in this community where they are restricted to the encruster guild, subordinate to tabulate and rugose corals and the chaetetid *Litophyllum koninckii*. Bafflers are dominated by dendroid tabulate corals, possibly inherited from the vertically (and hence laterally adjacent) coralline packstone facies.

CEPHALOPOD ASSOCIATION. This 'association' occupies the micritic carbonate facies, in the deeper shelf zone. It is a depauperate fauna consisting of scattered nautiloids, including *Diademoceras* rare atrypids, particularly *Desquamatia* sp., and rare ramose alveolitid fragments, tentatively assigned to *Cladopora* sp. The association represents a mixing of nektonic cephalopods and benthic forms which sporadically grew on the sea floor at the limits of the photic zone.

## BIOGEOGRAPHIC RELATIONSHIPS

Blodgett, Rohr, & Boucot (1990) remarked that the poorly known Givetian gastropods from Australia indicate a high degree of endemism, but this was based on only the study of Heidecker (1959). Work subsequent to 1990 has demonstrated that whilst this comment is essentially true, there are some affinities with Old World faunas. The bivalve *Tanaodon louderbacki* was first described from Sichuan and is also known from Guangxi, China (Kirk, 1927; Pojeta, 1986). Modiomorphs are common elements to both Old World and Eastern Americas Realms, during the Givetian. Indeed *Phenacocyclas* suggests Eastern Americas realm affinities. Of the gastropods *Burdikinia, Austerum* are known only from the adjacent Broken River Province, but *Labrocuspis* has been reported from the Kitikami Mountains in Japan (Kase, 1989). Preliminary observations of small collections the smaller gastropod fauna from the other parts of the Burdekin Formation suggests high numbers of murchisoniids, which suggest old world Givetian affinities (Blodgett, Rohr & Boucot, 1990).

The Givetian was a time of maximum cosmopolitanism for stromatoporoids, more so than for brachiopods and rugose corals (Stock 1990). At a generic level, the Burdekin stromatoporoid fauna shows strong affinities with faunas of the Old World Realm rich in

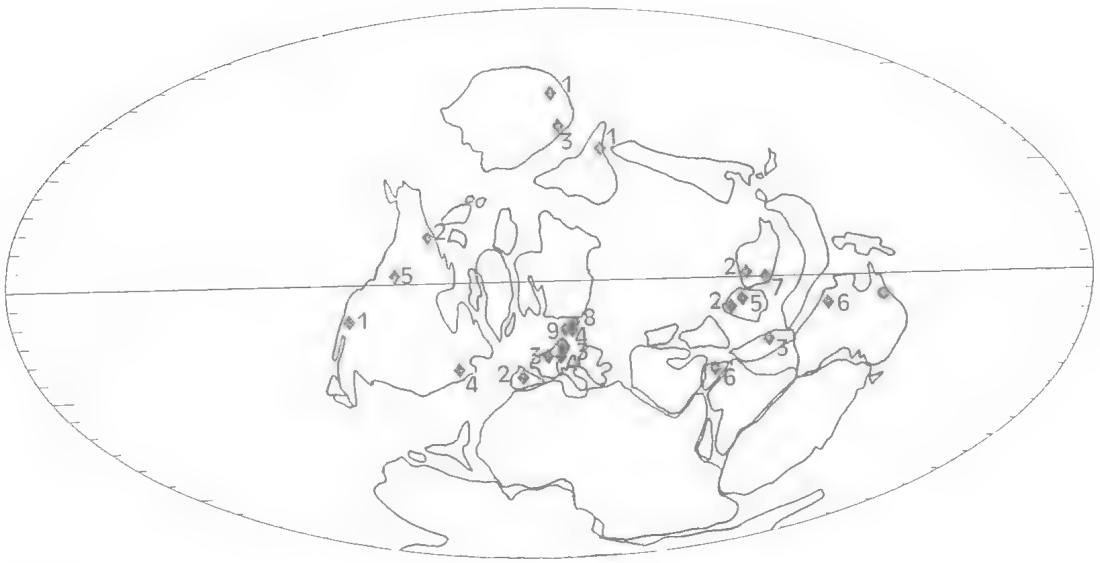


FIG. 17. Palaeobiogeographic affinities of the Burdekin stromatoporoid fauna showing the distribution of species found within the Burdekin fauna with numbers indicating the number of species common to both Burdekin and other localities. Reconstruction and localities follow Stock (1990) and McKerrow & Scotese (1990) for the Givetian time.

amphiporids, clathrodictyids, stromatoporids and syringostromellids.

Generic level affinities of the fauna are difficult to assess given its cosmopolitan nature. Based on the material confidently assigned to species, greatest affinities are with faunas from Guangxi, Poland, and Belgium but elements of the fauna are known from many other, mostly Old World, faunas (Fig. 17). There is considerable affinity with Givetian to Frasnian faunas worldwide.

Comparison with the adjacent Broken River Province is difficult given the limited studies of Mallett (1968, et seq.). Re-examination of Mallett's collections and additional material from the Broken River area is being undertaken by Webby & Zhen (pers. comm.) and has been published in part (Webby & Zhen 1997) who recognise modest numbers of *Salairella* species within the Middle Devonian assemblage. Examination of spot collections and the material of Mallett (1968) indicates that there are some similarities with the Burdekin fauna but proper evaluation must await completion of the work being undertaken by Webby and Zhen.

Preliminary assessment of Broken River spot collections is as follows:

Spanner Limestone Member Papilio Formation, Givetian (*varcus* zone)

Taxa present: *Stromatopora huepschii*
*Coenostroma* sp.
*Salairella buecheliensis*
*Salairella* sp.
*Actinostroma* sp.
*Clathrocoilona* sp.

Stanley Limestone member of the Mytton Formation-Late Givetian (*disparilis* zone)
*Stromatopora huepschii*
*Salairella buecheliensis*
*Salairella* sp.
*Actinostroma* sp.
*Hermatostroma* sp. cf. *H. schluteri*
*Hermatostroma* sp. cf *H. epsicopale*
*Clathrocoilona* sp. cf. *Clathrocoilona solida*
*Stachyodes* sp.
Dosey Limestone, Eifelian to Givetian
*Stromatopora huepschii*
*Salairella* sp.
?*Actinostroma* sp.
?*Trupetostroma* sp.
*Gerronostroma* sp.
*Salairella* sp. cf. *S. cooperi.*

Mallett (1968) recorded a large number of taxa from the 'Couvinian' to Givetian Dip Ck and Chinamans Ck Limestones, but only a few of these were ever published (Mallett, 1970a,b; 1971). Unpublished taxa include a number of species of *Stromatopora* including *S. huepschii*,

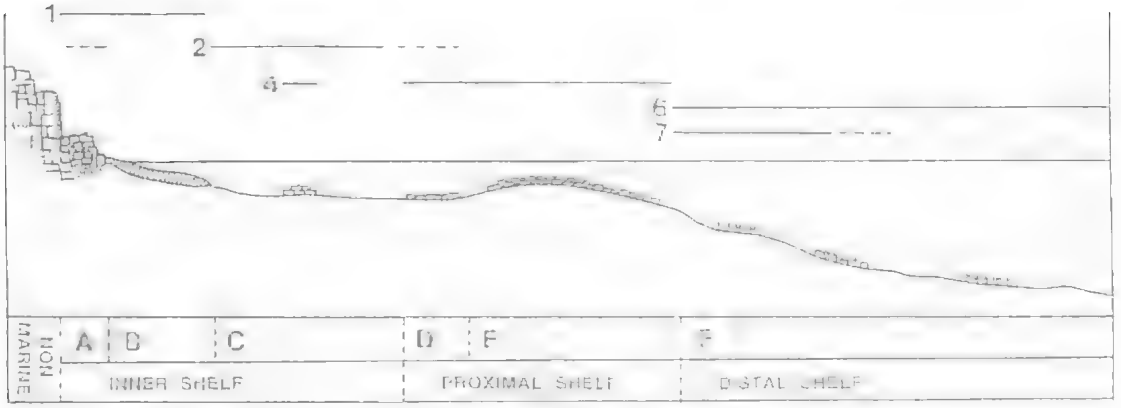



FIG. 18. Shelfal sedimentary assemblages and community distribution for deposition of the Big Bend Arkose and Burdekin Formation for the Fletcherview-Burdekin Downs area. 1, *Burdikinia* community; 2, *Stachyodes-Syringopora* community; 3, *Clathrocoilona spissa-Aulopora* community; 4, *Gerronostroma hendersoni-Hermatostroma maculatum* community; 5, *Ferestromatopora heideckeri-Amphipora-Stringocephalus* community; 6, *Amphipora pervesiculata* community; 7, *Hermatostroma episcopale- Coenostroma* community; 8, cephalopod association. A, abraded fossil, coarse siliciclastic facies; B, fossiliferous sandstone facies and impure limestone/ sandstone facies; C, nodular limestone facies; D, coverstone subfacies; E, facies of the biohermal complex; F, coralline packstone facies.

*A. ramosa* (also mentioned by Jell, 1967), *Stromatopora (Ferestromatopora) tyrganensis* Yavorksy, *Gerronostroma 'concentricum'*, a number of species of *Hermatostroma, Stictostroma, Anostylostroma* and *Actinostroma*. Brief examination of collections from this unit confirms the presence of *Salairella, Stromatoporella, Atelodictyon* and *Trupetostroma*. Mallett (1968, 1970a,b, 1971) recorded a number of *Actinostroma* species, most of which remain unpublished, within the Dip Ck and Chinamans Ck Limestone compared with the single species known from the Fanning River Group.

Webby & Zhen (1997) have recently published some of their taxonomic work based on Mallett's and additional materials. They record are *Actinostroma clathratum* Nicholson, *Aculatostroma* sp. *Nexililamina dipcreekensis* Mallett, *Hermatostroma malletti* Webby & Zhen, *Trupetostroma? tubulosum* (Mallett) and *Amnestostroma steloges* (Mallett) from the upper Eifelian to ?lower Givetian Dip Ck Limestone; *Actinostroma clathratum* Nicholson and *Hermatostroma malletti* Webby & Zhen from the upper part of the Chinaman Ck Limestone (early Givetian), and *Gerronostroma* sp. and *Stachyodes costulata* Lecompte from the Stanley Limestone Member of the Mytton Formation which is latest Givetian in age. From this it is clear that there are some specific differences and commonalities between the Burdekin and Broken River faunas, as would be expected. Perhaps differences could be accounted for by the difference palaeogeographic settings and the slight age differences between the described taxa. The Broken River carbonate platforms were more open marine conditions in comparison to the restricted embayed nature of the Burdekin Basin.

Zhen (1991) discussed the affinities of the abundant rugose coral fauna of the Fanning River Group. He recognised significant similarities with late Early to Middle Devonian faunas from Germany, southwest China, northwest China, south China and the Urals, and recognised other affinitites with central Asia, Vietnam and North America. Zhen (1991) also noted similarities with New South Wales and north Queensland rugose coral faunas, but assessment of the relationships of these faunas awaits systematic assessment of their stromatoporoids.

## CONCLUSIONS

Ten faunal communities are recognised based on the study and distribution of stromatoporoid and selected mollusean taxa, and the distribution of tabulate and rugose corals. These communities vary according to the 2 styles of shelf assemblage. The specific relationships between the facies of Cook (1995) and the communities here presented is given in Figs 18 and 19. The *Burdikinia* community is a robust gastropod-

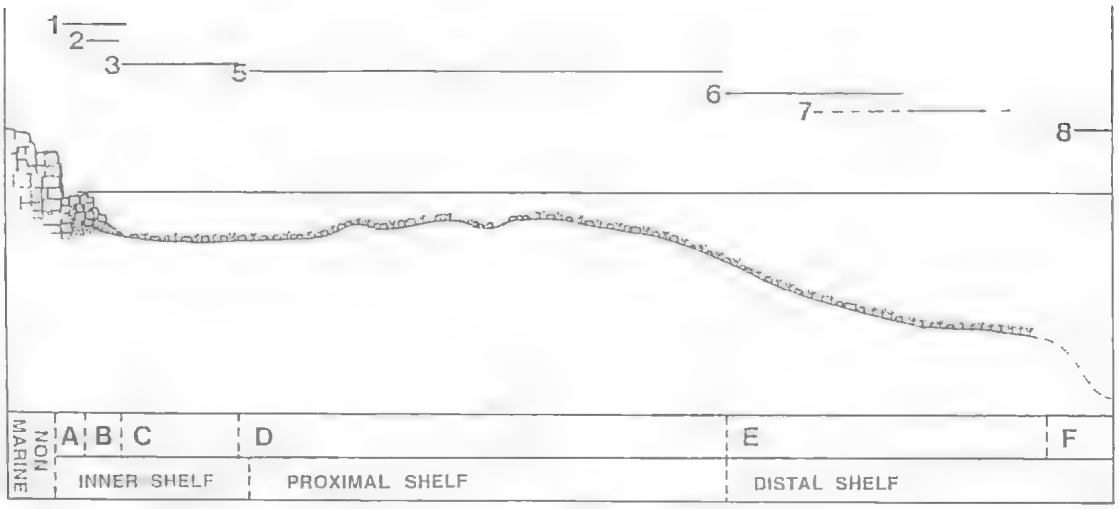



FIG. 19. Shelfal sedimentary assemblages and community distribution for deposition of Big Bend Arkose and Burdekin Formation for deposition of the Big Bend Arkose and Burdekin Formation for the Fanning River area. 1, *Burdikinia* community; 2, *Stachyodes-Syringopora* community; 3, *Clathrocoilona spissa-Aulopora* community; 4, *Gerronostroma hendersoni-Hermatostroma maculatum* community; 5, *Ferestromatopora heideckeri-Amphipora-Stringocephalus* community; 6, *Amphipora pervesiculata* community; 7, *Hermatostroma episcopale-Coenostroma* community; 8, cephalopod association.
A, abraded fossil, coarse siliciclastic facies; B, fossiliferous sandstone facies; C, fossiliferous siltstone and innermost silty biostromal facies group; D, facies of the biostromal complex; E, coralline packstone facies; F, micritic carbonate facies.

dominant community which occupies the coarse siliciclastic inner shelf, and the *Modiomorpha* community occurs as a rare but distinctive in situ shell bed. The *Stachyodes costulata-Syringopora* community occurs within inner shelf muddy impure carbonate lagoons, but elements were able to inhabit interstitial niches in subtidal marine headlands. In the Fletcherview-Burdekin Downs area, the *Hermatostroma maculatum-Gerronostroma hendersoni* community inhabited patch reefs in the inner shelf, backreef laminar stromatoporoid pavements and the main reefal environments. The *Clathrocoilona spissa-Aulopora* community occupied nearshore, fringing biostromes in the Fanning River area. The *Ferestromatopora heideckeri-Amphipora ramosa-Stringocephalus* community occupied extensive nearshore to offshore biostromes within the Fanning River-Golden Valley areas whereas the *Coenostroma-Hermatostroma episcopale* community dwelt within dispersed stromatoporoid pavements and, more sparsely, within offshore coralline thickets. The *Amphipora pervesiculata* community dominated dendroid stromatoporoid-coralline thickets adjacent to and seaward of bioherms, dispersed stromatoporoid pavements and stromatoporoid biostromes particularly in the Fletcherview-Burdekin Downs area. The *Endophyllum* community was restricted to patch reefs which grew during regressive phase, carbonate to siliciclastic transition. The cephalopod association is represented by a sparse fauna found within deeper water, micritic carbonate facies in the Golden valley area.

Within the Kirkland Downs area, poor preservation prevents accurate assessment of the stromatoporoid fauna, but biostromal deposits are dominated by colonial rugose corals, in addition to elements probably related to the *Ferestromatopora-Amphipora ramosa-Stringocephalus* community.

Stromatoporoid shape is controlled by both ecologic and genetic factors. Interactions of sedimentation rate, substrate type and availability, depositional energy and siliciclastic input demonstrably influence shape. Many stromatoporoid taxa display shape ranges rather than restricted gross morphologies.

The distribution of taxa indicates that most stromatoporoids occupied a range of environments on the shallow shelf, but some, such as *Amphipora ramosa*, were more restricted in their distribution.

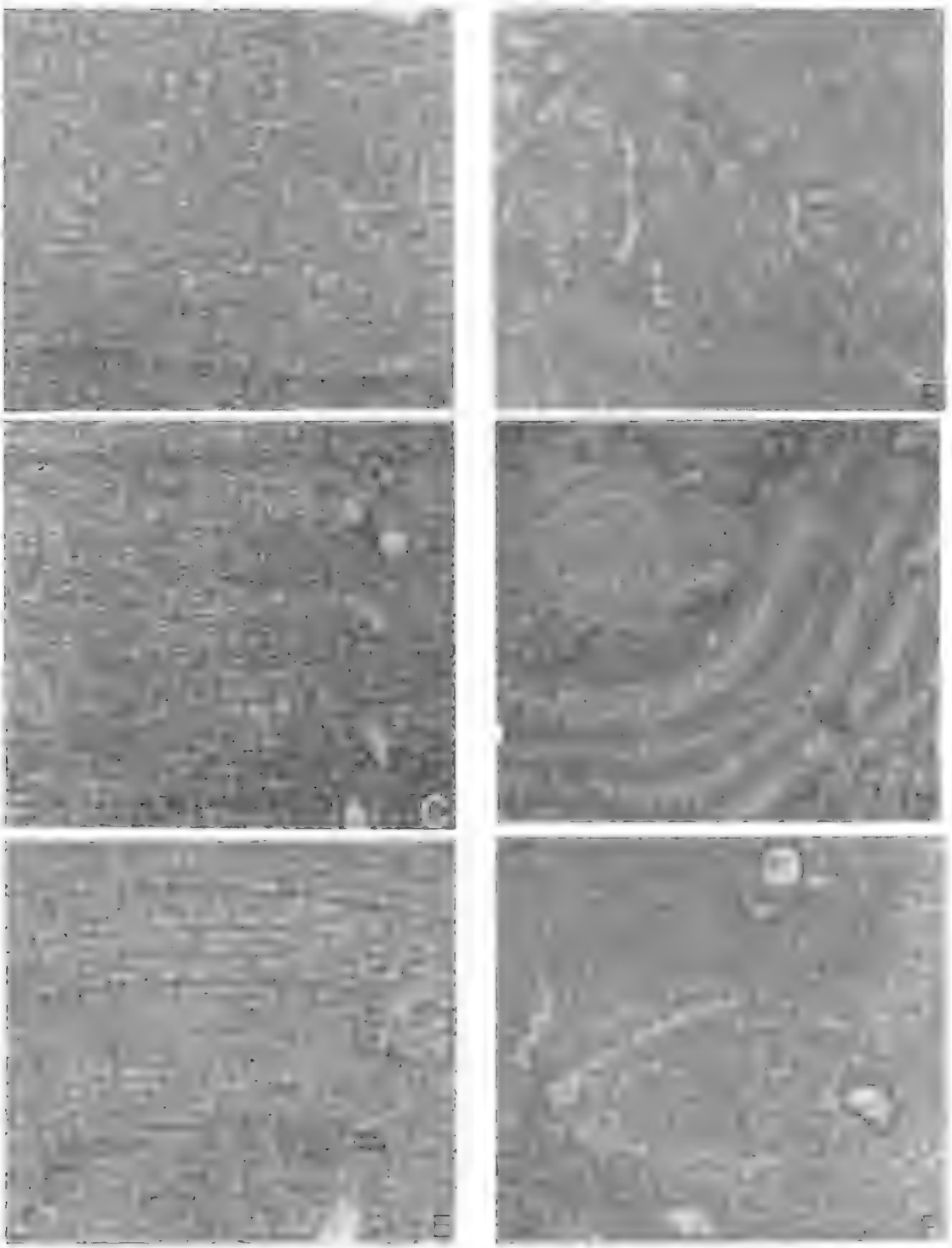


FIG. 20. *Actinostroma filitextum* Lecompte, 1951. A, B, JCUF11935 × 10. Section. C, D, JCUF11939 × 10. E, F, JCUF11879 × 10. A, C, E, vertical section. B, D, F, tangential section.

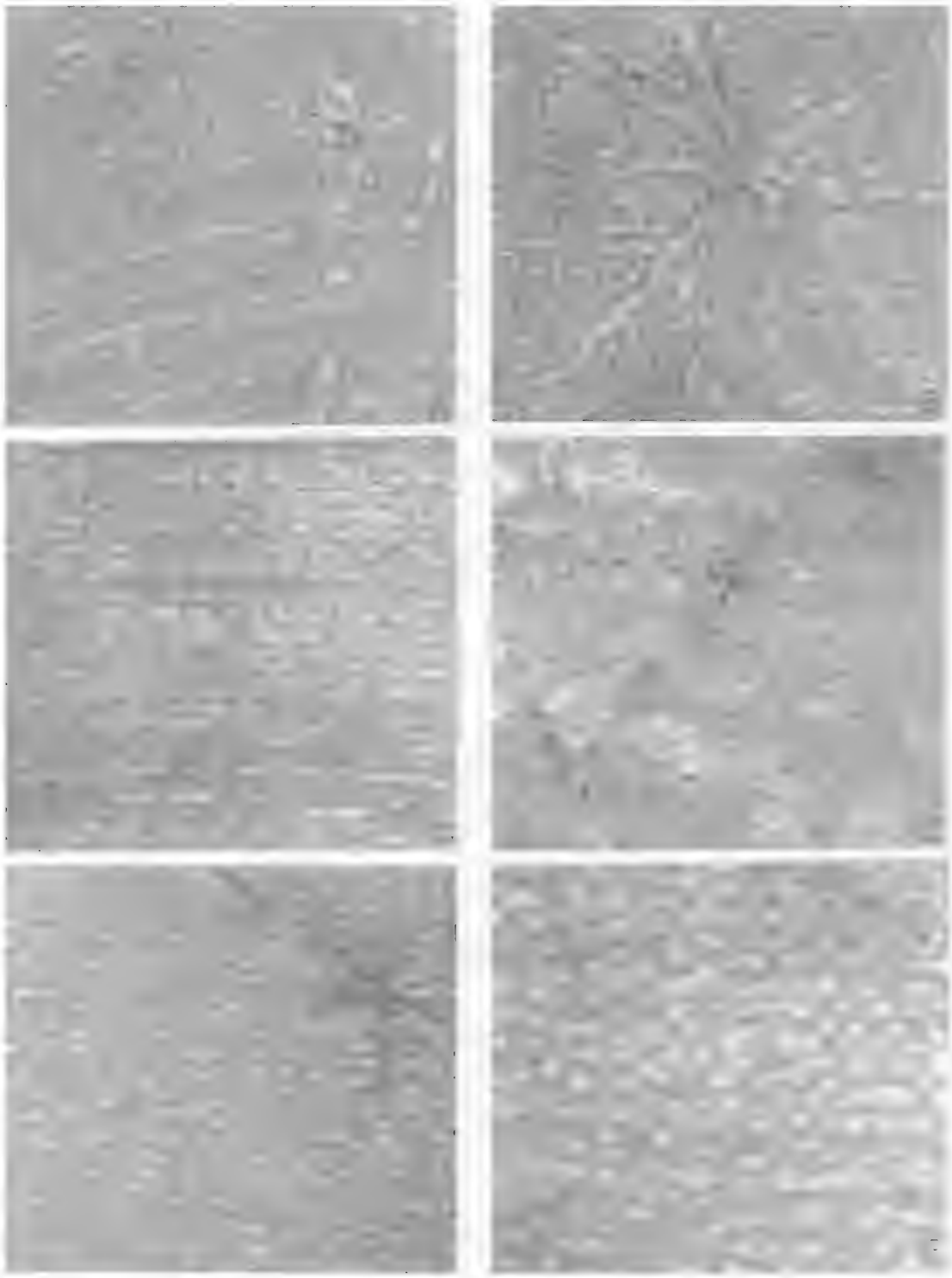


FIG. 20. A, B, *Icmosoma tiliaetum* Lecompte, 1951, JCUF11881 — 10. A, vertical section; B, tangential section. C,D, *Ichthyostroma* sp. JCUF11942 — 10. C, vertical section; D, tangential section. E, F, *Clathrochaeta* sp. JCUF12004. E, vertical section — 10; F, vertical section — 20.

Overgrowth phenomena occur within most depositional environments of the Burdekin Formation, but particularly complex and common overgrowths were found within nearshore, siliciclastic-dominant biostromal units at Fanning River. This situation is interpreted to represent preservation of the organisms from a biostrome that had been stressed by the effects of nearshore siliciclastic sedimentary processes.

Stromatoporoid intergrowths are common within the fauna, particularly those involving *?Syringoporella* sp, which is associated with stromatoporoids with more irregular skeletal architecture. Distribution of *?Syringoporella* sp. is regular, and skeletal response by their host stromatoporoids is evident. The absence of micritic envelopes on tabulate walls suggests that the coral growth surface matched that of the stromatoporoid host. Other intergrowths include sporadic *Syringopora*? sp., a number of rugose corals and symbionts allied to *Helicosalpinx* sp.

Designation of guild membership within communities has required adaptation of the reefal guild structure concept of Fagerstrom (1987) to allow for non-reefal, biostromal communities. Some taxa demonstrated guild overlap between facies.

Taxonomic analysis of the fauna has determined the presence of 35 stromatoporoid taxa, of which 6 are previously undescribed. Fourteen species are left in open nomenclature.

Bivalves and gastropods show Old World Realm affinites and the stromatoporoid fauna shows strongest affinities with Early to Middle Devonian faunas in China, Europe, Germany, France and Late Devonian reefal faunas in Western Australia.

## SYSTEMATIC PALAEONTOLOGY

PORIFERA Grant, 1836
STROMATOPOROIDEA
Nicholson & Murie, 1878
ACTINOSTROMATIDA
Bogoyavlenskaya, 1969
ACTINOSTROMATIDAE
Nicholson, 1886b

### **Actinostroma** Nicholson, 1886b

*Actinostroma* Nicholson, 1886b: 75; Lecompte 1951: 67; Galloway & St. Jean 1957: 148; Galloway 1957: 437; Stearn 1966a: 86; Flügel & Flügel-Kahler 1968: 522; Kazmierczak 1971: 129; Zukalová 1971; Mallett 1971: 235; Yang & Dong 1979: 30; Stearn 1980: 888; Stock 1982: 669; Stock 1984: 774; Bogoyavlenskaya & Khromych 1985: 66.
*?Trigonostroma* Bogoyavlenskaya 1969: 463 (transl.).
*Bullatella* Bogoyavlenskaya 1977b: 13.
*Auroriina* Bogoyavlenskaya 1977b: 16.
*Lamellistroma* Bogoyavlenskaya 1977b: 17.

TYPE SPECIES. *A. clathratum* Nicholson, 1886a by original designation from Gerolstein, Middle Devonian of Germany.

DISTRIBUTION AND AGE. Silurian to Late Devonian (Frasnian), widespread in Old World Realm and found in Eastern Americs Realm from the Givetian (Flügel & Flügel-Kahler, 1968; Stearn, 1979; Cockbain, 1989).

REMARKS. Identification of the hexactinellid network is critical to the definition of the genus. Although it is variably developed and preserved (Stearn, 1966; Mistiaen, 1985), most authors regard it as a fundamental character. Sleumer (1969) argued for a much wider concept of the genus to include non-hexactinellid forms like *Gerronostroma* Yavorksy. Although variable preservation of the network is evident in Burdekin material, even within single slides, the network is regarded as a vital generic character, and Sleumer's (1969) wide generic concept is hence rejected.

Flügel & Flügel-Kahler (1968) recorded over 100 species for the genus, and Bogoyavlenskaya & Khromych (1985) recorded an additional 5 taxa. New species assigned to *Actinostroma* by Chinese authors include 3 described by Yang & Dong (1979) and 5 from Dong, Wang & Fu (1989). Cockbain (1984) has contributed one new species from the Canning Basin, W.A. The large number of species of this genus is testament not only to its wide spatial and temporal distribution, but also to the reluctance of some authors to 'lump'. Most taxa of *Actinostroma* have been differentiated on the basis of laminae and pillar spacings (see Lecompte, 1951; Flügel, 1959; Mallett, 1971). Use of 'art-feld' diagrams (Flügel, 1959) and gallery indices (Klovan, 1966; Mallett, 1971; Cockbain, 1984) have further quantified characters differentiating species. Strict use of statistical tools for the differentiation of stromatoporoid taxa must take account of the high degree of variation (Cockbain, 1979; Stearn, 1989). Stearn (1989) argued that the species concept in stromatoporoids is generally too narrow and that the use of average measured skeletal parameters will not be useful in species determination unless the measured structures are homologous. However, most authors do not

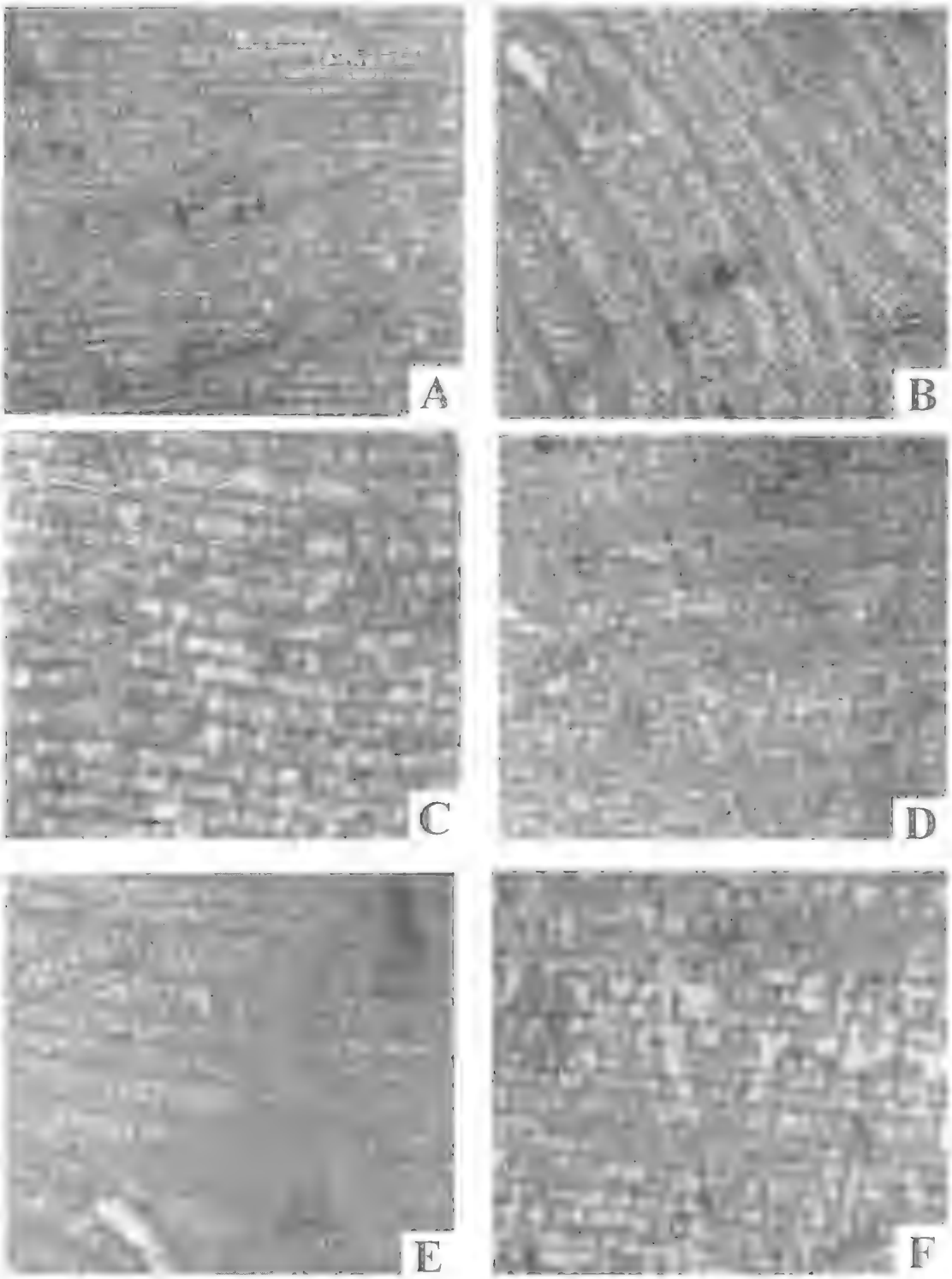



FIG. 22. *Atelodictyon fallax* Lecompte, 1951. A-C, JCUF11882. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20. D-F, JCUF11883. D, vertical section × 10; E, tangential section × 10; F, vertical section × 20.

detail how measured skeletal parameters were derived; it can only be assumed that measurements are from similar parts of the skeleton. Cockbain (1984) used pillar and laminar spacings and a gallery index (a reciprocal of Klovan's 1966 index) to synonymise *A. papillosum* (Bargatzky), *A. clathratum* Nicholson, *A. subclathratum* Etheridge Jr and *A devonense* Lecompte allowing for a wide species concept. Mistiaen (1985) disagreed with this synonymy maintaining *A. clathratum*, *A. papillosum* and *A. devonense* as distinct taxa. Webby & Zhen (1993) questioned the status of *A. papillosum* given its inadequate illustration. Relationships among these taxa will be a matter of continued debate.

This work adopts a wide species concept for *A. filitextum* Lecompte, allowing for a range of morphometric values. *A. filitextum* Lecompte, *A reversum* Lecompte and probably *A. perlaminatum* Lecompte are considered to be synonymous, representing a gradation through delicately constructed actinostromid morphology.

Stearn (1980) has discussed the synonymy of *Trigonostroma* Bogoyavlenskaya 1969, *Bullatella* Bogoyavlenskaya 1977b, *Auroriina* Bogoyavlenskaya 1977b and *Lamellistroma* Bogoyavlenskaya 1977b. Bogoyavlenskaya & Khromych (1985) record no further use of these genera beyond their original descriptions. Webby (pers. comm.) has kindly pointed out that *Trigonostroma* is possibly a coral, and hence is a highly doubtful synonym.

**Actinostroma filitextum** Lecompte 1951
(Figs 20, 21A,B.)

?1951 *Actinostroma perlaminatum* Lecompte: 120, pl. 12, fig. 4; Mistiaen: 48, pl. 2, figs. 4-5.
1951 *Actinostroma filitextum* Lecompte: 121 pl 13, fig. 1; Mistiaen 1985:46, pl. 1, figs. 8-10, pl. 2, fig. 6.
1951 *Actinostroma reversum* Lecompte: 121 pl.13, fig. 2.
?1963 *Actinostroma cf. filitextum* Lecompte: Yang & Dong: 152 (170 trans.), pl. 4, figs. 5-6.

MATERIAL. JCUF11877-81, 11935-7, ?11939-41, 11842, from JCUL778, JCUF11934 from float near JCUL778, JCUF11942-3 from JCUL787.

DESCRIPTION. Form apparently medium domical, known from only fragments up to 100mm high and 160mm wide. Skeleton with variably spaced latilaminae. Thick (0.04-0.10mm), continuous pillars which intersect many laminae spaced 16-26 per 5mm (mean = 21.3, σ=2.2) joined in a hexactinellid network or rounded in cross-section. Laminae composed of joined colliculi, typically gently undulating, uncommonly strongly undulose, and variably discontinuous; thinner than pillars; (0.03-0.05mm thick) spaced 27-37 per 5mm (mean = 30.2, σ=2.1). Hexactinellid network moderately-well developed. Astrohizae present, 5-8mm apart, stellate, with distal dichotomous branching of longer canals. Skeletal material compact.

MORPHOMETRICS. This and subsequent tables present data as mean (σ = standard deviation), N=10 unless otherwise specified, P5= pillars per 5mm, Pt= pillar thickness, L5, laminae per 5mm, Lt= laminar thickness.

| Specimen | P5 | Pt | L5 | Lt |
|---|---|---|---|---|
| JCUF11877 | 22.8 (1.9) | 0.09 (0.02) | 31.4 (1.8) | 0.04 (0.02) |
| JCUF11878 | 20.2 (2.2) | 0.04 (0.02) | 28.4 (1.8) | 0.03 (0.01) |
| JCUF11879 | 21.8 (2.4) | 0.09 (0.01) | 28.8 (2.6) | 0.05 (0.01) |
| JCUF11880 | 21.4 (2.2) | 0.09 (0.03) | 32.1 (2.3) | 0.04 (0.01) |
| Average | 21.6 (2.2) | 0.08 (0.02) | 30.2 (2.1) | 0.04 (0.01) |

DISTRIBUTION AND AGE. Burdekin Basin, north Queensland, Australia, Givetian; ?Gueizhou, China, Eifelian; Dinant Basin, Belgium, ?Givetian and Frasnian; Afghanistan, Late Devonian.

REMARKS. The characteristic continuous pillars and obvious hexactinellid network confirm the Burdekin material as *Actinostroma*. The large range of pillar and collicular spacings demonstrates the high degree of variation within the specimens, given that all data came from the middle of skeletons. The material is characteristic of the delicate architecture of *A. filitextum* Lecompte and is assigned to that species. *A. crassepilatum* Lecompte and *A. reversum* were differentiated from *A. filtiextum* by collicular spacing, the thicker pillars, and astrorhizal characteristics (Lecompte, 1951: 121) although the latter must be regarded as a dubious for separation. Whilst *A. crassepilatum* has markedly thicker pillars, *A. reversum* has pillars only a little thicker. *A. perlaminatum* has very closely spaced pillars and laminae, and may represent an extreme morphotype; a tentative synonymy is suggested.

**Aculatostroma** Khalfina, 1968

TYPE SPECIES. *Syringostroma verrucosum* Khalfina, 1961 from the Lower Devonian, Salair, Siberia, by subsequent designation.

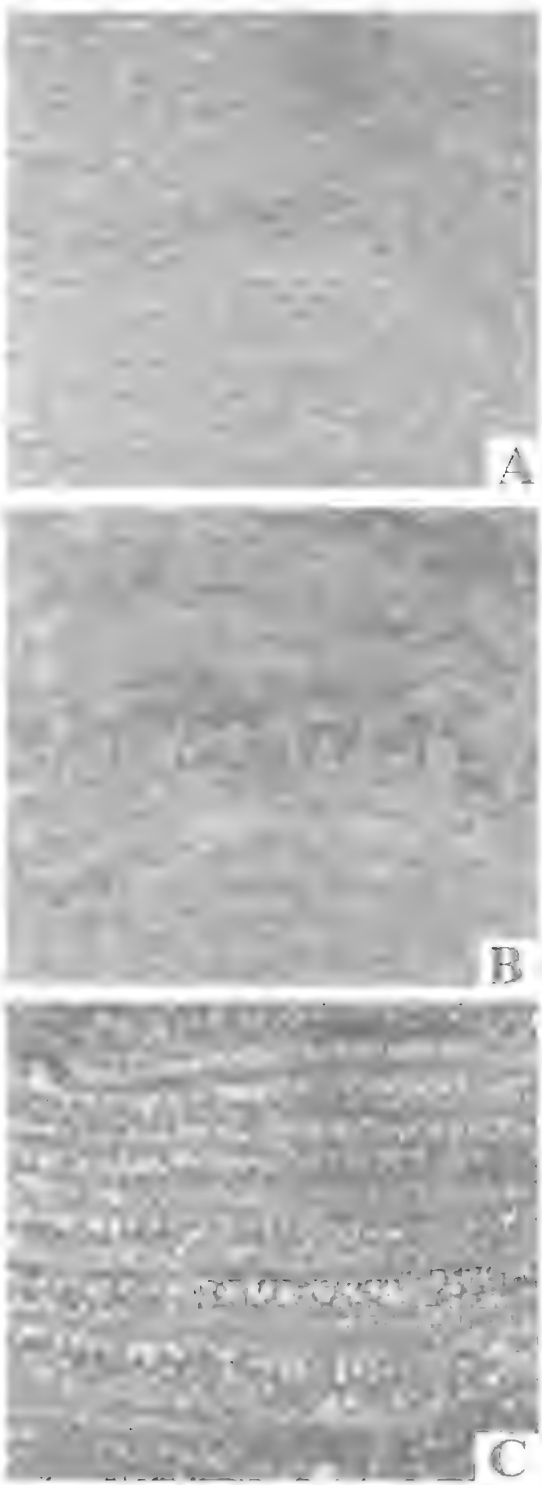



FIG. 23. *Schistodictyon* sp. JCUF12014. A, vertical section × 10; B, vertical section × 20; C, oblique tangential section × 10.

REMARKS. Stearn (1991) has provided a synonymy and a full discussion of the genus. Webby, Stearn & Zhen (1993) recorded a doubtful taxon from the Lower Devonian of Victoria.

**Aculatostroma?** sp.
(Fig. 21C,D)

MATERIAL. JCUF11942-3 from JCUL787.

DESCRIPTION. Two fragmental specimens from laminar skeletons; laminae dominant, straight to very gently undulose, generally persistent; approximately 10-11 per 2mm,variable in thickness, but thin (0.02-0.05mm). Pillars slightly thicker, 0.02-0.08mm, very irregularly spaced so that measurement is difficult. Pillars commonly branch in interlaminar space or flare upwards to form colliculate laminae. Both laminae and pillars are composed of compact skeletal material. Dissepiments common in irregular, horizontally elongate galleries. In tangential section the skeletal elements are poorly preserved. Short pillar chains are evident, and pillars are rarely isolated. Simple walled astrorhizae are present.

REMARKS. The upward flaring of pillars to form colliculate, but persistent, laminae suggests assignment to *Aculatostroma* Khalfina. The poor preservation of tangential section and the relative persistence of laminae leaves the generic assignment open to question.

CLATHRODICTYIDA
Bogoyavlenskaya, 1969
CLATHRODICTYIDAE Kühn, 1939
**Clathrodictyon** Nicholson & Murie, 1878

*Clathrodictyon* Nicholson & Murie 1878: 220; Flügel & Flügel-Kahler 1968: 534; Bogoyavlenskaya & Khromych 1985: 72; Stearn 1991: 617.

TYPE SPECIES. *Clathrodictyon vesiculosum* Nicholson & Murie, 1878 from the Early Silurian of Ohio, U.S.A. by original designation.

DISTRIBUTION AND AGE. Worldwide, Ordovician to Late Devonian.

REMARKS. A recent review and synonymy of the genus was provided by Stearn (1991) and Flügel & Flügel-Kahler (1968) provided an earlier, comprehensive synonymy.

**Clathrodictyon** sp.
(Fig. 21E,F)

MATERIAL. JCUF12004, single specimen from JCUL782.

DESCRIPTION. Single fragment from a low domical skeleton greater than 2cm thick and 5cm wide. In vertical section laminae long, compact and downwardly inflected to form pillars, with a gentle chevroned appearance, spaced approximately 9-11 per 2mm, of variable thickness (0.02-0.08mm). Pillars short, not superposed, formed by inflections of laminae, spaced approximately 7-10 per 2mm, generally slightly thicker (0.02-0.10mm) than laminae. Galleries horizontally elongate, somewhat lenticular, or rounded. No dissepiments or astrorhizal traces were seen. Skeletal material compact.

REMARKS. Characteristic inflection of laminae to produce pillars, and the lenticular galleries are characteristic of *Clathrodictyon*. Assignment of species affinities requires more extensive material.

**Atelodictyon** Lecompte 1951

*Atelodictyon* Lecompte 1951: 124; Flügel & Flügel-Kahler 1968: 529; Fischbuch 1969: 169; Zukalová 1971: 40; Khromych 1974: 31; Stearn 1975b: 1646; Khromych 1976: 46; Mistiaen 1980: 188; Bogoyavlenskaya & Khromych 1985: 69; Stearn 1991: 618.

Not *Atelodictyon* Lecompte, Galloway & St Jean 1957: 122; Galloway 1957: 435; Stearn 1966a: 87; Kazmierczak 1971: 127; Stearn 1980: 894; Stock 1982: 661; Mistiaen 1985: 54.

TYPE SPECIES. *Atelodictyon fallax* Lecompte, 1951 from the Middle Devonian of Belgium by original designation.

DISTRIBUTION AND AGE. Worldwide, Early to Late Devonian.

REMARKS. Stearn (1991) has discussed the particular problems of this genus. In addition to the taxa listed by Stearn (1991) as belonging in *Atelodictyon*, *A. dewalense* Mistiaen, 1985 appears to be a valid designation. *A. connectum* Yang & Dong, 1979 (Plate 4, fig 7,8) shows somewhat discontinuous laminae and is probably not *Atelodictyon*.

**Atelodictyon fallax** Lecompte 1951
(Fig. 22)

*Atelodictyon fallax* Lecompte 1951: 125, pl. 15, figs 1a-d: Galloway & St. Jean 1957: 122, pl. 6: Flügel & Flügel-Kahler 1968: 156: Fischbuch 1969: 169, pl.1, figs 1-5: Yang & Dong 1979: 22, pl. 4, figs.1-4: Dong et al. ?1989: 265, pl. 7, figs. 1a,b.

MATERIAL . JCUF11882- 84, 11886-89, 12003 all from Fanning River type section JCUL788.

DESCRIPTION. Skeleton medium domical, latilaminate. Laminae continuous, gently undulose spaced 20-26 per 5mm (mean =24 , n= 10), relatively thin (0.08- 0.12mm). Pillars 25-35 (mean = 30.8, n=10) per 5mm, thin (0.08-0.16mm) commonly superposed or complex in vertical section, forming chain-like network in tangential section. Astrorhizal canals common, sporadically crossed by dissepiments. Skeletal material compact.

DISTRIBUTION AND AGE. Burdekin Basin, North Queensland, Givetian; Alberta, Canada, Givetian; Dinant Basin, Belgium, Eifelian; Guangxi, China, Eifelian.

REMARKS. Continuous laminae, characteristic chain-like pillar cross sections and their variability in interlaminar space are identical with *A. fallax* Lecompte. Preservation in some specimens is poor, with parallel zones of skeleton obliterated. Thus only a small sample was available for morphometric study. *Atelodictyon lazutkini* (Yavorsky, 1955) has less well developed vertical elements. *A. obscurum* (Yavorsky, 1955) has more tortuous pillars in interlaminar space. *A. durum* (Khromych, 1974) has pillar and laminar spacings approaching that of the Burdekin material, but the chain structures do not appear as elongate in the figure provided by Khromych (1974: pl. 15, fig 1.). *A. latitextum* Wang in Wang et al. (1986) has a more amalgamate appearance in tangential section. This taxon has thicker laminae than *A. hickense* Webby, Stearn & Zhen 1993 from the Lower Devonian of Victoria.

**Schistodictyon** Lessovaya,
in Lessovaya & Zakharova 1970

TYPE SPECIES. *S. posterius* from the Upper Silurian Isfra Beds, Turkestan, by original designation.

REMARKS. Stearn (1991) and Bogoyavlenkaya & Khromych (1985) have provided a discussion and synonymy for this genus. Webby, Stearn & Zhen (1993) have recorded a doubtful representative of this genus from Victoria, Australia. Stearn (1991) discussed *Nexililamina* Mallett, from north Queensland as a possible synonym.

**Schistodictyon** sp.
(Fig. 23)

MATERIAL. JCUF12014 from L 781.

DESCRIPTION. Single fragment of a low domical skeleton greater than 4cm wide and 3cm

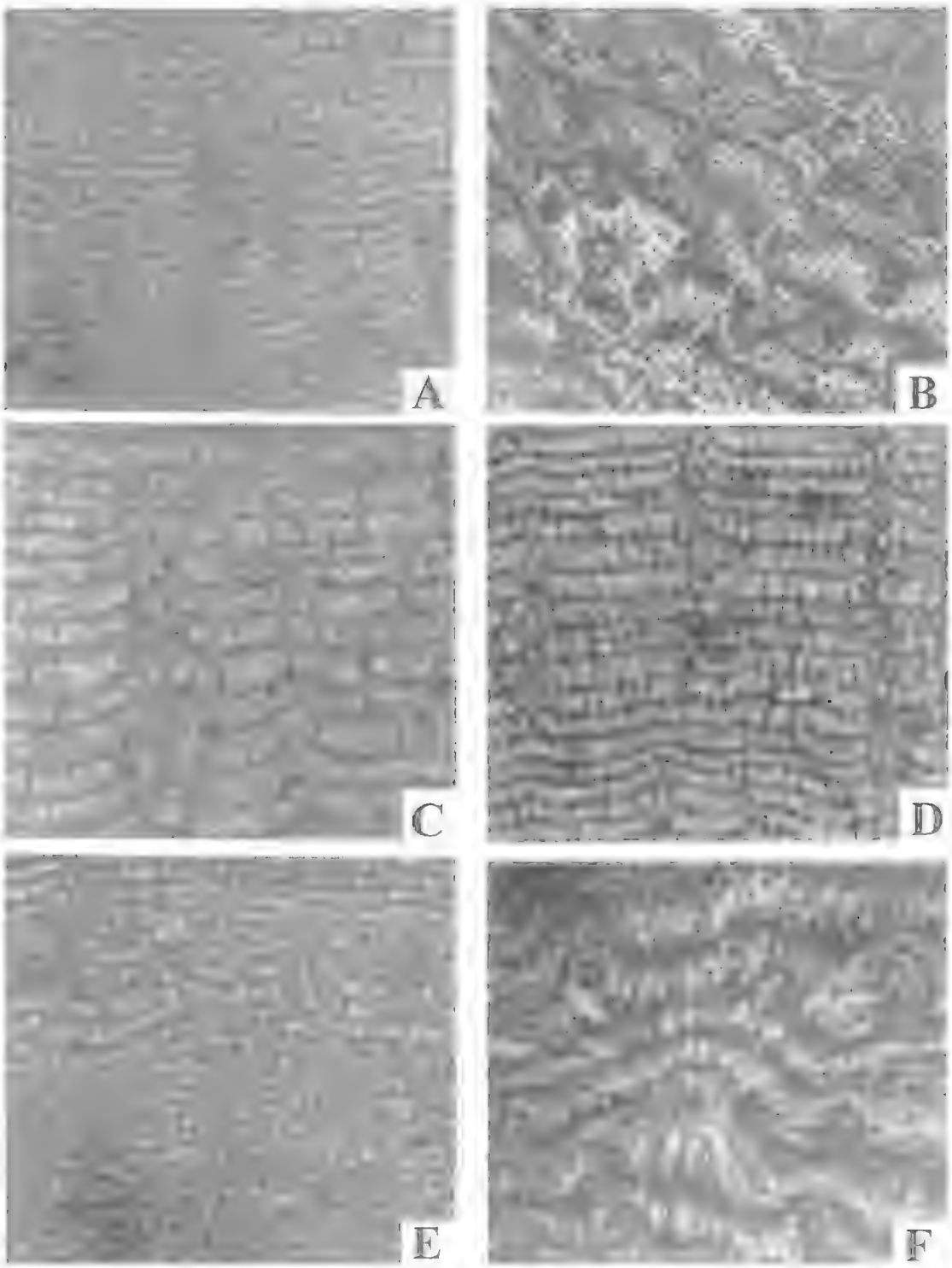



FIG. 24. *Gerronostroma hendersoni* sp. nov. A-C, holotype JCUF11955 × 10. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D, paratype JCUF10817, vertical section × 10; E, F, paratype JCUF11956 × 10; E, vertical section; F, tangential section.

thick. Laminae straight to gently undulose, continuous, each comprised of a dark thin compact line. Laminae 4-7 per 2mm, 0.02-0.05mm thick, highly variably spaced, highlighting thin latilaminae,. Pillars short, not superposed, highly complex within interlaminar space, being multiply branched, commonly oblique, and spreading along the lower surfaces of laminae, irregularly spaced, 7-12 per 2mm, 0.02-0.08mm thick. Skeletal material compact. Galleries irregular, with an overall rectangular to rounded aspect. Weak astrorhizal traces present. There may be dissepiments but these are difficult to distinguish from the complex pillar branches.

REMARKS. Complex branching of pillars is typical of *Schistodictyon*. The specimen lacks the obvious dissepiments of *Pseudoactinodictyon* and the branching is far too simple for *Anostylostroma*. The laminae are not formed by colliculi such as in *Aculatostroma*. *Anostylostroma?* sp. of Mistiaen (1985) is similar in aspect and should be reassigned to *Schistodictyon*. *Nexililamina dipcreekensis* Mallett is of doubtful generic identity (Stearn, 1991), but possible assignment to *Schistodictyon* has been suggested (Stearn, 1980, 1991). It has much simpler interlaminar branching of pillars.

### **Gerronostroma** Yavorsky 1931

*Gerronostroma* Yavorsky 1931: 1406; Galloway & St. Jean 1957: 151; Galloway 1957: 438; Stearn 1966a : 101; Flügel & Flügel-Kahler 1968: 545; Yang & Dong 1979: 37; Stearn 1980: 889; Bogoyavlenskaya & Khromych 1985: 77; Mistiaen 1985: 127; Stearn 1990: 494; Stock, St. Jean & Otte 1990: 4; Webby & Zhen 1993: 332.
*Clathrostroma* Yavorsky 1960:
*Gerronodictyon* Bogoyavlenskaya 1969: 20.
*Praeldiostroma* Bogoyavlenskaya 1969: 108.
*? Gerronostromina* Khalfina & Yavorsky 1971, 119.
*?Imponodictyon* Khalfina & Yavorsky 1971: 119.

TYPE SPECIES. *Gerronostroma elegans* Yavorsky, from the Middle Devonian of the Kuznets Basin, Russian Federation by subsequent designation of Galloway & St.Jean (1957).

DISTRIBUTION AND AGE. Old World Realm, Silurian (Ludlow) to Late Devonian (Frasnian).

### **Gerronostroma hendersoni** sp. nov.
(Figs 24, 25A)

ETYMOLOGY. For Professor Robert Arthur Henderson, of James Cook University, Townsville, for his contribution to the palaeontology of north Queensland, and to this study.

MATERIAL. HOLOTYPE: JCUF11955 from JCUL781. PARATYPES: JCUF11944, 11945, 11946, 11949, 11950, 11956 from JCUL778; JCUF11948, 11951, 11952, 11958, 11965, 11967, 11969, 11970 from JCUL779; JCUF 1194, 11953, 11954, 11957, 11959, 11961, 11962, 11964, 11968, 11971, 11972, 11975 from JCUL781; JCUF11960 from JCUL784; JCUF11963, 11966 from JCUL788; JCUF11973, 11974 from JCUL795.

DIAGNOSIS. *Gerronostroma* with laminae spaced 6-10 in 2mm, pillars 6-11 in 2mm; with commonly inflected laminae, with inflections giving rise to small persistent tubes and common dissepiments which may be locally continuous.

DESCRIPTION. Skeleton laminar, low or medium domical, up to 140mm high and 200mm wide, some material fragmental. Commonly latilaminate with latilaminae 2-5mm thick. Astrorhizae common, inconspicuous to absent in hand specimen, revealed in tangential section as complex but small (3-9mm wide), with no observed partitions within canals. Vertical sections consist of strongly to weakly undulose laminae, locally inflected. These upturnings sporadically form continuous vertical tubes which traverse many laminae. Laminae continuous, spaced 6 to 10 in 2mm (mean = 8.04, $\sigma$= 1.08, N=50),0.02mm to 0.15mm thick (mean = 0.10, $\sigma$=0.03, N=50); single-layered and compact or transversely fibrous. Pillars superposed through up to 10 laminae forming a grid, and consist of compact or fibrous skeletal material, spool-shaped, 0.03 to 0.13 mm thick (mean =0.1, $\sigma$=0.04, n=50), spaced 6 to 11 in 2mm (mean =8.6, $\sigma$=1.5, n=50). Galleries are slightly vertically elongated. Gently arcuate to near straight dissepiments are present in interlaminar spaces of some specimens, where they may be locally continuous producing microlaminae. Others are more arcuate and discontinuous.

In tangential section pillars rounded or coalesced to short vermicular in form. Laminar intersections a continuous sheet, rarely pierced by pores. Laminar inflections, where present are evidenced by complex ring structures 0.3-1.2mm across (mean =0.7, $\sigma$=0.3, n=21), or where inflections are up to one interlaminar space in height, simple rings resembling ring pillars (mean =0.32, $\sigma$=0.06, n=23) are apparent.

MORPHOMETRICS.

| Specimen | L2 | L1 | P2 | P1 | n |
|---|---|---|---|---|---|
| JCUF11951 | 8.1(0.9) | 0.09(0.03) | 7.3(1.5) | 0.10(0.03) | 10 |
| JCUF11954 | 8.4(0.7) | 0.08(0.02) | 8.3(1.2) | 0.08(0.03) | 10 |
| JCUF11955 | 7.9(1.2) | 0.06(0.04) | 9.0(1.2) | 0.11(0.03) | 10 |
| JCUF11957 | 7.3(1.1) | 0.10(0.03) | 9.4(1.2) | 0.12(0.05) | 10 |
| [illegible] | [illegible] | 0.12(0.05) | 9.0(1.2) | 0.11(0.04) | 10 |
| Average | 8.0 (1.0) | 0.09 (0.03) | 8.6 (1.3) | 0.10 (0.04) | - |

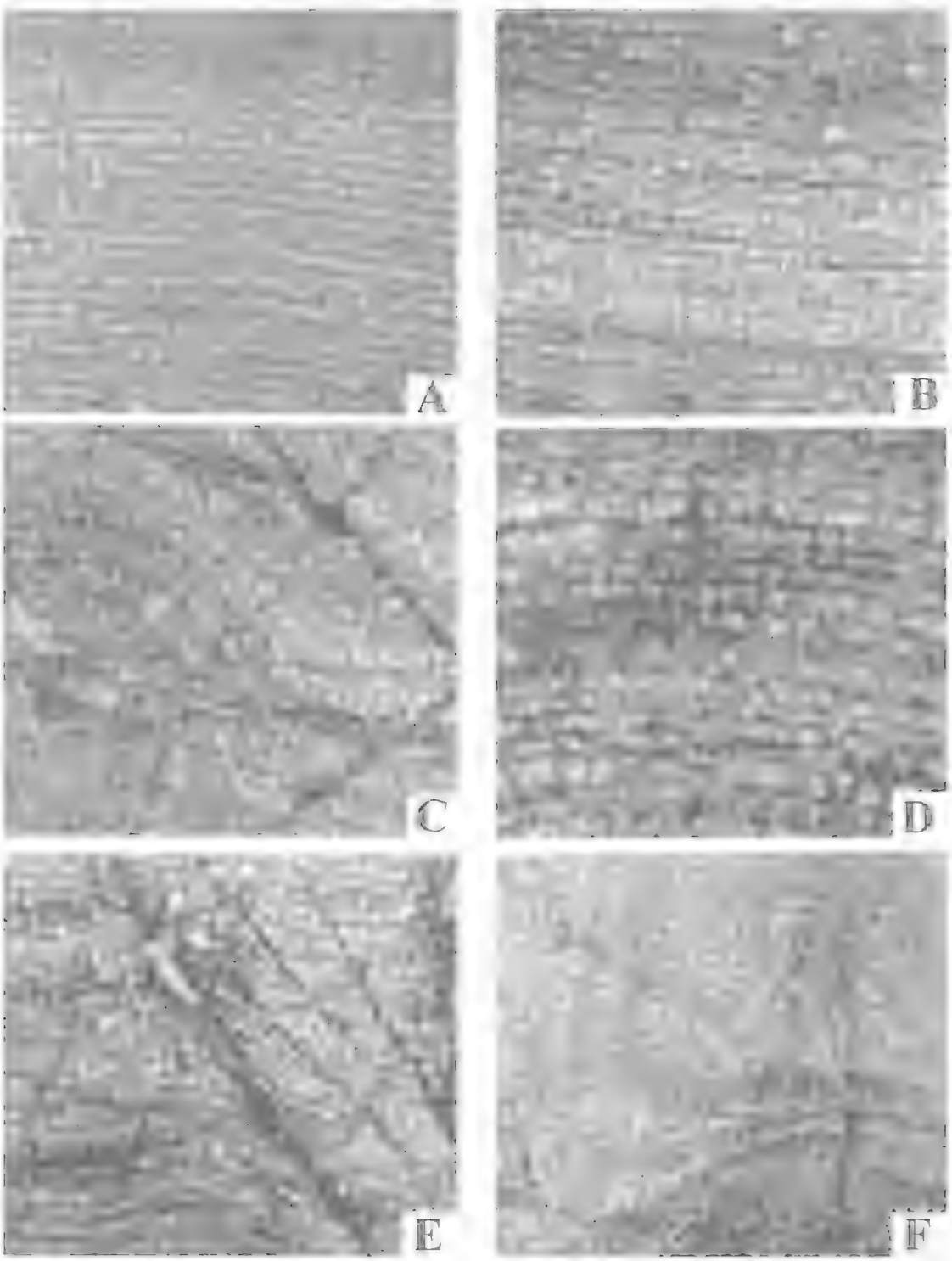



FIG. 25. A, *Gerronostroma hendersoni* sp. nov. Paratype JCUF11973, vertical section ×10. B-F, *Gerronostroma* sp. B-D, JCUF11978. B, vertical section × 10; C, tangential section × 10; D, vertical section × 20. E, F, JCUF11977. E, vertical section × 10; F, tangential section × 10.

DISTRIBUTION AND AGE. Burdekin Formation, north Queensland, Middle Devonian, Givetian.

REMARKS. The regular grid, persistent laminae and spool-shaped, superposed pillars, clearly identify *Gerronostroma* Yavorsky. Burdekin material differs from other *Gerronostroma* by pillar and laminar spacings, laminar inflections and the slightly elongate galleries. Species closest to this taxon are *Gerronostroma* cf. *G. immemoratum* Bogoyavlenskaya of Stearn (1983) which resembles the Burdekin material in element spacing, but lacks the inflected laminae, and the common dissepiments. *G. immemoratum* Bogoyavlenskaya is also comparable, but also lacks the laminar inflections. The published illustrations (Bogoyavlenskaya 1977b) are too poor for an adequate assessment of relationships.

Presence of 3 orders of tube-like structures within specimens is problematic. Ring pillars are regarded as a generic character of *Stromatoporella* Nicholson, but the regular superposition of the pillars, and the absence of tripartite laminae in the Burdekin material excluded this genus. Persistence of these tubes in vertical section suggests that they may represent a very simple astrorhizal tube, with no radiating canals. If this were so then they may be of little taxonomic value. In addition one may expect a gradation from small tubes to complex canal systems. More complex ring structures are expressions of small mamelons, clearly represented in vertical section, and the largest order structure is naturally the astrorhizae. There is no ontogenetic development from small tubes through complex rings to astrorhizae in this material, and they are not gradational features. Some laminar inflections associated with the small tubes are half to one laminar interspace in height, and are best regarded as expressions of micromamelons on the contemporary surface. Others show no relief from their contemporary surfaces and are problematic.

**Gerronostroma** sp.
(Fig. 25B-F)

MATERIAL. JCUF11977-82, 12009, 12015-6. All from JCUL788 except JCUF11979 from JCUL779 and JCUF11982 from JCUL781.

DESCRIPTION. Low to medium domical skeleton. Two specimens show intergrowth with rugose corals (JCUF12016 with cf. *Stringophyllum* sp. and JCUF11978 with an unidentified form). Latilaminae are inconspicuous, between 1-2mm thick, with a basal zone of more closely spaced laminae. Adjacent to coral intergrowths in JCUF12016 the grid becomes highly disorganised and skeletal structure becomes a dense complex array of elements. In vertical section, pillars and laminae form a regular grid. Laminae continuous, slightly undulose, or locally undulose suggesting low mamelons, 8-11 per 2mm and 0.02-0.08mm thick. Pillars mostly continuous, through up to 7 laminae, but sporadically they are restricted to interlaminar space, commonly slightly spool-shaped between laminae, spaced 8-11 per 2mm, 0.02-0.08mm thick. Galleries equidimensional to slightly vertically elongate, rectangular with common rounded corners; no dissepiments were seen within them. In tangential section pillars isolated to short vermiform. Laminar intersections appear as sweeping arcuate zones of dense material sporadically pierced by irregular voids. In JCUF12016, where intergrown with rugose corals, the pillars are poorly preserved but show irregular form and spacing; mostly vermiform and a little narrower in cross-section. Astrorhizae small and simple with a central rounded axial canal and up to 4 short, thick simple radiating canals lacking dissepiments. Skeletal material, although not very well preserved appears to be compact.

REMARKS. The species differs from the type by the spacing of pillars and laminae, and in *G. elegans* Yavorksy the pillars are 2-3 times thicker than the laminae. *G. hendersoni* sp. nov. has fewer pillars and laminae per 2mm, problematic tubular structures, and possesses dissepiments. *G. vergens* Webby & Zhen, 1993 from the Emsian Jesse Limestone, New South Wales, has similar pillar-laminar spacing but possesses more prominently V-shaped pillars. Due to the indifferent preservation of this material, the taxon is left in open nomenclature.

**Anostylostroma** Parks, 1936

TYPE SPECIES. *Anostylostroma hamiltonense* by monotypy, from the Middle Devonian Traverse Group, Michigan, U.S.A.

REMARKS. A recent review has been presented by Stearn (1991) and further comment is unnecessary.

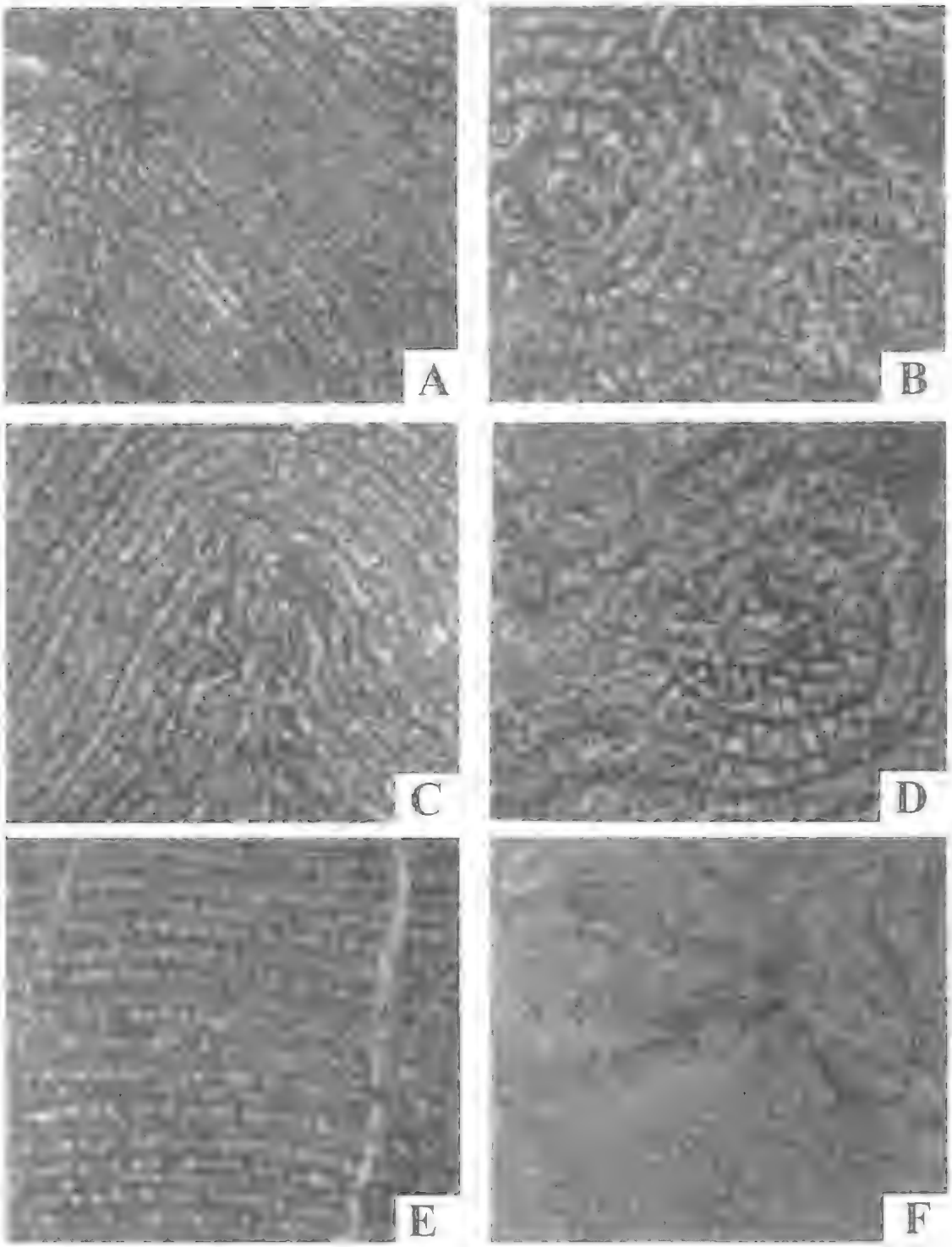



FIG. 26. A-D, *Anostylostroma ponderosum* (Nicholsun, 1875) JCUF11379 × 10. A, C, vertical section; B, D, tangential section. E, F, *Anostylostroma* sp. JCUF12005 × 10. E, vertical section; F, tangential section.

**Anostylostroma ponderosum**
(Nicholson, 1875)
(Fig. 26A-D)

*Stromatopora ponderosa* Nicholson 1875:. 246, pl. 24, figs. 4,4a,4b.
*Clathrodictyon ponderosum* Parks 1936: 42, pl. 5, figs. 5,6.
*Anostylostroma ponderosum* (Nicholson) 1957: Galloway & St. Jean: 111, pl. 4, figs. 2a, 2b; Fagerstrom 1962: 425, pl. 65, figs. 1-8; Stearn & Mehotra 1970: 6, pl 1, figs. 1,2; Kazmierczak 1971: 81,pl 14, figs. 2a,2b,3; Cockbain 1984: 24, pl. 8a-8d.

MATERIAL. JCUF11379-82 all from JCUL778.

DESCRIPTION. Material consists of fragments derived from low domical to laminar skeletons, weakly latilaminate. Continuous, strongly undulating, laminae relatively thin, average 13 per 5mm, average thickness 0.07mm. Pillars in some cases superposed and flaring upwards, some branch in interlaminar spaces, approximately 16-17 per 5mm, varying greatly in thickness (average 0.07mm). Dissepiments very common, but not omnipresent. Tissue compact. Mamelon columns very prominent 13-17mm apart showing a variable diameter. In vertical section the skeletal elements within columns merge, intertwine, commonly fuse and inflected upwards. Columns appear as a disorganised collection of vertical vermiform 'tubes.' Intercolumnar skeleton comprises somewhat vermiform pillars which distributed 9-10 per 1mm$^2$. Astrorhizal canals present but inconspicuous and are found within mamelon columns.

MORPHOMETRICS.
P1$^2$= number of pillars per 1mm square in tangential section

| Specimen | P2 | L2 | Pt | Lt | P1$^2$ |
|---|---|---|---|---|---|
| JCUF11379 | 6.5 | 5.2 | 0.07 | 0.07 | 10.6 |
| JCUF11380 | 7.2 | 6.8 | 0.10 | 0.12 | 8.0 |
| JCUF11381 | 6 | 5.6 | 0.08 | 0.07 | 9.6 |
| JCUF11382 | 8 | 5.4 | 0.06 | 0.11 | 9.2 |

DISTRIBUTION AND AGE. Canning Basin, Western Australia, Frasnian; Burdekin Subprovince, north Queensland, Givetian; Holy Cross Mountains, Poland, Frasnian; Italy, Middle Devonian; Ohio and Michigan, Middle Devonian; Ontario, Canada, Middle Devonian; Northwest Canada, Frasnian.

REMARKS. The flaring and/or branching of the pillars in interlaminar space and the characteristic mamelon columns places the specimens within *Anostylostroma ponderosum* (Nicholson). Fagerstrom (1982) and Cockbain (1984) have discussed the synonymy of *A. ponderosum* and *A. laxum*. The solution to the problem of types suggested by Cockbain (1984) remains unresolved; no type has, as yet, been chosen from the type locality. Morphometric data indicated some degree of variation within the species with JCUF11380 and JCUF11382 possessing thicker skeletal elements and representing specimens that have experienced more pronounced diagenetic effects. A similar phenomenon was reported for the genus by Fagerstrom (1982).

**Anostylostroma** sp.
(Figs 26E,F, 27A,B)

MATERIAL. JCUF12005-7, 12010-13, ?JCUF12008 all from JCUL788

DESCRIPTION. Skeletal shape medium domical up to 7cm thick and 12cm wide; some smaller fragmental material. Astrorhizae inconspicuous in hand specimen. Latilaminae present but not obvious, 0.8-3.0cm thick. Laminae and pillars form a regular grid in vertical section. Laminae thin, 0.02-0.08mm thick, continuous, dark and compact, 6-10 per 2mm Pillars compact, mostly superposed forming a grid, straight or commonly branched in interlaminar space into a y-shape or flaring along the base of laminae, thicker than laminae (0.05-0.10mm), 8-10 per 2mm. Galleries rectangular to irregular, lacking dissepiments. Astrorhizal axial canals wide, generally straight, with thick compact strongly arcuate dissepiments. In tangential section pillars very rarely isolated, mostly forming short linked chains of short vermiculae. Arcuate laminar intersections are somewhat diffuse. Astrorhizae inconspicuous, consisting of scattered walled radial canals with few dissepiments and wide circular intersections of axial canals.

REMARKS. Predominance of superposed pillars in this taxon suggests reference to *Gerronostroma* but the common Y-shaped pillars indicates affinities to *Anostylostroma* whose type species also has superposed pillars. *G. vergens* Webby & Zhen has similarly y-shaped pillars in a comparable network. Webby & Zhen (1993) suggested their taxon may be *Schistodictyon*, but that genus is characterised by far more complexly branched pillars. *G. vergens* may well represent *Anostylostroma*, despite its regular skeletal network. Poor preservation of all the available material

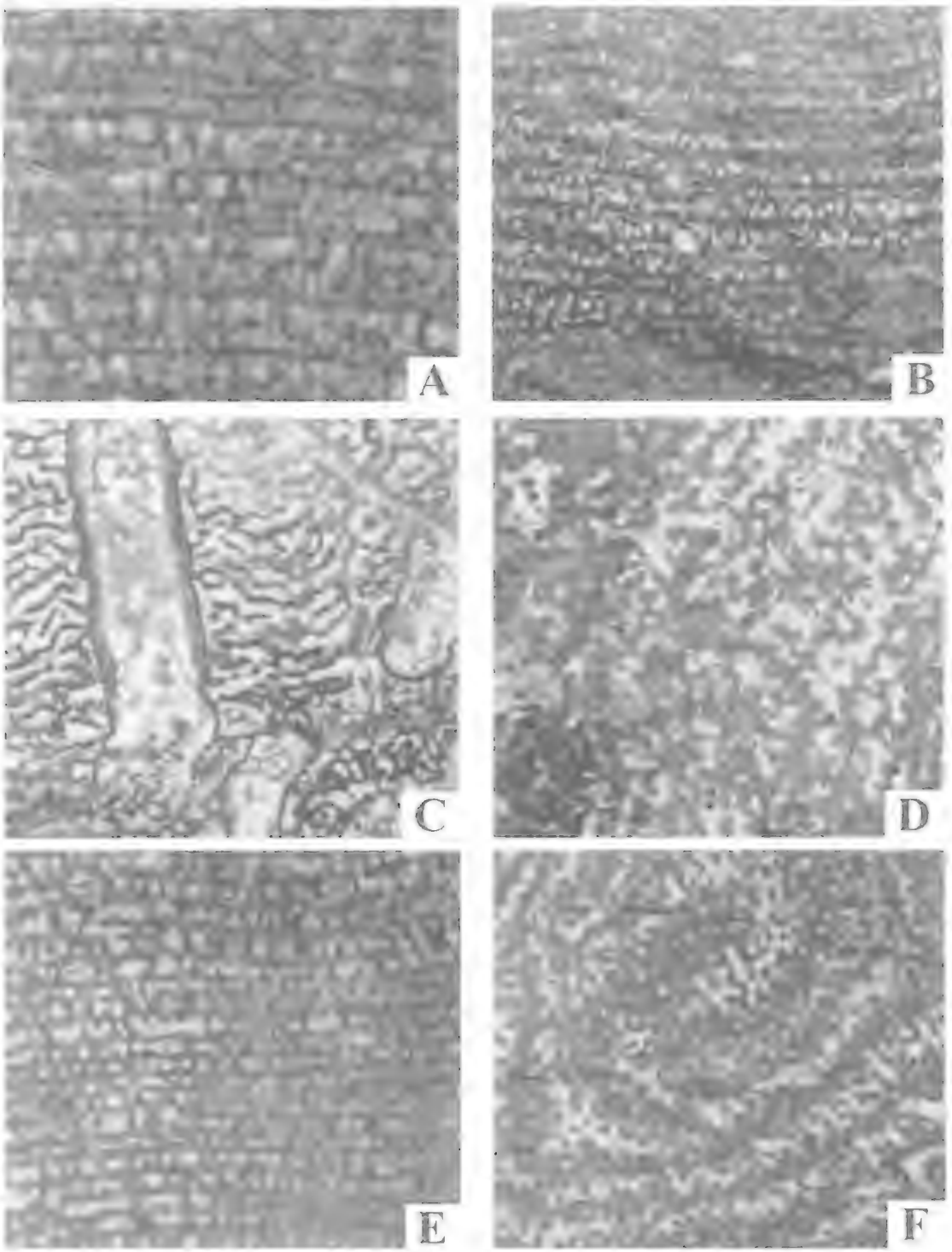



FIG. 27. A, B, *Anostylostroma* sp. A, JCUF12005, vertical section × 20; B, JCUF12006, oblique-vertical section × 10. C, D, Gen. et. sp. indet. cf. *Clathrodictyella* sp. JCUF11378 × 10. C, vertical section; D, tangential section. E, F, *Stictostroma* sp. JCUF11976 × 10. E, vertical section; F, tangential section.

precludes proper definition of this taxon but the unusual style of regular network suggests reference to a new species.

Genus et species indet. cf. **Clathrodictyella** sp.
(Fig. 27C,D)

MATERIAL. JCUF11378 from JCUL778.

DESCRIPTION. Small fragment of a presumably laminar skeleton possessing a symbiotic tabulate coral of syringoporid affinity. Prominent, thick, discontinuous laminae, undulatose and locally chevroned throughout, 12 to 13 per 5mm and are 0.08 to 0.2mm thick; weakly inflected giving off a few, generally thinner, variable pillars confined to one interlaminar space. Pillars spaced 6-7 per 5mm, 0.05-0.15mm thick, cateniform in tangential section. Microstructure mostly compact with a very weak fibrous nature.

REMARKS. This single specimen does not relate well to all other specimens within the Burdekin collections. Professor Colin Stearn (pers. comm.) has viewed copies of the illustrations herein and suggested a relationship to *Clathrodictyella* Bogoyavlenskaya or *Novitella* Bogoyavlenskaya whose species are mostly cylindical in skeletal shape. The specimen is referred tentatively to *Clathrodictyella* on the basis of the gross skeletal element morphology, but the problem of a non-cylindrical skeleton remains unresolved.

STROMATOPORELLIDA Stearn, 1980
STROMATOPORELLIDAE
Lecompte, 1952

**Stictostroma** Parks, 1936

TYPE SPECIES. *Stictostroma mammiliferum* Galloway & St. Jean, 1957 (cf. Fagerstrom 1977).

**Stictostroma** sp.
(Fig. 27E,F)

MATERIAL. JCUF11976.

DESCRIPTION. Skeletal shape very low domical with maximum height 30mm maximum width 170mm, terminal surface gently undulose; with scattered small astrorhizae. In vertical section the skeleton is dominated by relatively continuous, undulating laminae spaced 14-17 per 5mm, sporadically pierced by pores. Laminae 0.15-0.20mm thick, conspicuously tripartite with upper and lower margins of compact material separating a light axial zone. Laminae commonly have, coalesced with their margins, circular, hollow 'pustules' approximately 0.15mm in diameter projecting slightly into interlaminar space.

Pillars not superposed, confined to, and commonly not completely crossing, interlaminar space; in many places oblique. Where complete they are spool-shaped, commonly flare upwards or rarely divide, thicker than laminae (0.15-0.3mm) and spaced irregularly at 10-18 per 5mm. Pillars consist of compact to flocculent skeletal material. Galleries irregular, elongate with rounded boundaries, commonly crossed by thin dissepiments. In tangential section pillars rounded to short and vermiform; rare ring-pillars present. Sections through laminae highlight regular, rounded foramina and rarely a light median zone. Astrorhizae are complex, wide, with a centre of regular pillars and laminae and long thick radiating arms not obviously traversed by dissepiments.

REMARKS. The rare presence of ring pillars, the tripartite laminae and non-superposed pillars clearly identifies the specimen as *Stictostroma*. Lack of additional material precludes specific assignment despite the well preserved nature of the specimen and it is left in open nomenclature pending more material.

**Clathrocoilona** Yavorsky, 1931

*Clathrocoilona* Yavorsky 1931: 1394; Yavorsky 1955: 38; Galloway & St. Jean 1957: 221; Galloway 1957: 451; Galloway 1960: 634; Stearn 1962: 14; Stearn 1966a: 98; Stearn 1966b: 45; Birkhead 1967: 79; Stearn & Mehrotra 1970: 11; Zukalová 1971: 55; Khromych 1974: 36; Khromych 1976: 54; Kosareva 1976: 21; Dong & Huang 1978: 32; Yang & Dong 1979: 70; Stearn 1980: 891; Stock 1982: 670; Stock 1984: 776; Bogoyavlenskaya & Khromych 1985: 71; Mistiaen 1985: 94; Stock, St. Jean & Otte 1990: 3.
In Part *Stromatoporella* Nicholson, Lecompte 1952: 88.
In Part *Stromatopora* Goldfuss, Kazmierczak 1971: 88 .

TYPE SPECIES. *C. abeona* Yavorsky 1931 by monotypy from the Middle Devonian, S.W. Border of the Kuznetsk Basin, Russia.

DISTRIBUTION. Widely distributed, Eifelian to Famennian.

REMARKS. *Clathrocoilona* has been variably assigned to the Stromatoporellidae, Stromatoporidae, Clathrodictyidae and Stictostromatidae. The problematic relationship between it and like genera such as *Stictostroma*, *Stromatoporella*, and *Synthetostroma* stems from conflicting interpretations of the style and importance of microstructure. Macrostructural similarities between these latter 3 genera led Stearn (1980) to

include them all in the Stictostromatidae. *Stromatoporella* Nicholson possesses ring-pillars, and ordinicellular laminae (Stearn, 1966a). *Clathrocoilona* was separated from *Stictostroma* Parks on the basis of an arbitrary point in morphological gradient, *viz.* when the thickness of the laminae reaches the height of the galleries (Stearn, 1966a). *Synthetostroma* Lecompte was synonymised with *Clathrocoilona* by Kosareva (1976). This is in contrast to the views of Galloway (1957) who noted, as differences, the large number of microlaminae and the presence of superposed pillars in *Synthetostroma*. Lecompte's (1951) original diagnosis is clear: *Synthetostroma* has superposed pillars and cellular skeletal fabric, rather than the seldom superposed pillars and compact tissue of *Clathrocoilona*. Stearn (1980) did not support the opinions of Kosareva (1976), maintaining *Synthetostroma* as a separate genus. Stock, St. Jean and Otte (1990) noted Kosareva's (1976) view and commented that St. Jean disagreed with the synonymy. Given Lecompte's (1951) original diagnosis, it is clear that *Clathrocoilona* and *Synthetostroma* are separate genera.

Yavorsky (1931 & 1955) stressed the importance of the rounded galleries and the compact skeletal tissue for *Clathrocoilona* which combined with the characteristic tripartite laminae are essential to the concept of the genus.

**Clathrocoilona abeona** Yavorsky, 1931
(Fig. 28A,B)

*Clathrocoilona abeona* Yavorsky 1931: 1395, 1407, pl. 1, figs. 9-11, pl. 2, figs. 1,2,2a; Rukhin 1938p. 88, pl. 22, fig. 2; Galloway 1957 pl. 3,5, fig. 8; Galloway & St. Jean 1957: 222, pl. 21. fig. 3, pl. 23, fig. 1; Flügel & Flügel-Kahler 1968: 16; Fischbuch 1969: 180, pl. 13, figs. 1-5; Yang & Dong 1979: 71, pl. 39, figs. 5-6; Bogoyavlenskaya & Khromych 1985: 4.

? *Clathrocoilona abeona* Yavorsky, Galloway 1960: 634, pl. 77, fig. 2.

MATERIAL. JCUF 12059, 12063, 12748 and ? 12753 from JCUL778; JCUF 12060-12062, JCUF 12751, 12752 from JCUL781; JCUF 12749 from JCUL788; JCUF 12750 from Golden Valley, S of Fanning River Station.

DESCRIPTION. Skeletal shape laminar to low domical, with a large range in size up to 80cm wide and 8cm thick. Growth surface variably undulose, some specimens showing widely spaced (1-4cm), low mamelons. Specimens moderately, although not conspicuously, latilaminate with latilaminae thicknesses of 0.8-2.5cm. In vertical section skeletal elements form an irregular grid. Laminae continuous, gently to moderately undulose, sporadically upturned into mamelon columns within which they are difficult to separate from pillars, 3-6 per 2mm, thick (0.18-0.28mm), with a thin, central, light axis. Laminae divide sporadically along their length giving rise to new laminae. The central line similarly divides with the dividing laminae. Pillars are short, thick and spool-shaped, and may be superposed through 2-3 laminae, but in general confined to one interlaminar space. They are irregularly spaced across the laminae (3-6 per 2mm), thinner than laminae, but of variable thickness (0.05-0.25mm). Pillars and laminae are comprised of compact to flocculent tissue, with some suggestions of relict transverse fibrosity. Galleries irregular, rectangular, ovoid or rounded, and generally horizontally elongate; as thick as laminae. Dissepiments are common. Upturnings in laminae give rise to broad mamelon columns within which skeletal material is disordered. Two or more irregular vertical tubes form the vertical expression of the astrorhizae; which may be crossed by dissepiments. In tangential section laminar intersections dominate and consist of solid skeletal material with rare small pores; less commonly a trace of the central light line of the laminae is seen. Pillars are rounded, ovoid to very short, vermiform in cross section and are commonly joined by dissepiments. They commonly coalesce to form larger irregular pillar masses. At margins of laminae they coalesce with the solid skeleton. In tangential section astrorhizae are expressed as wide, diffuse radial sets of, in some places, long, walled thick canals, with or without dissepiments, eminating from a complex central mamelon column. There is no single centre, but a number of rounded central cavities.

DISTRIBUTION AND AGE. SW Kuznets Basin, Russia, Middle Den; Logansport Limestone, Indiana, Middle Devonian; Swan Hills Formation, Canada, Late Givetian; Mackenzie Valley, NWT, Canada, Frasnian.

MORPHOMETRICS.

| Specimen | L2 | Lt | P2 | Pt |
|---|---|---|---|---|
| JCUF12051 | 4.0 (0.5) | 0.21 (0.04) | 5.1 (0.7) | 0.15 (0.06) |
| JCUF12061 | 4.9 (0.7) | 0.20 (0.06) | 5.7 (1.3) | 0.13 (0.07) |
| JCUF12062 | 4.0 (0.6) | 0.23 (0.04) | 4.9 (0.7) | 0.18 (0.09) |
| JCUF12748 | 4.1 (0.5) | 0.19 (0.05) | 5.1 (1.1) | 0.13 (0.05) |
| Average | 4.3 (0.7) | 0.21 (0.05) | 5.2 (1.0) | 0.14 (0.07) |

REMARKS. This material is indistinguishable from that described by Yavorsky (1931), which

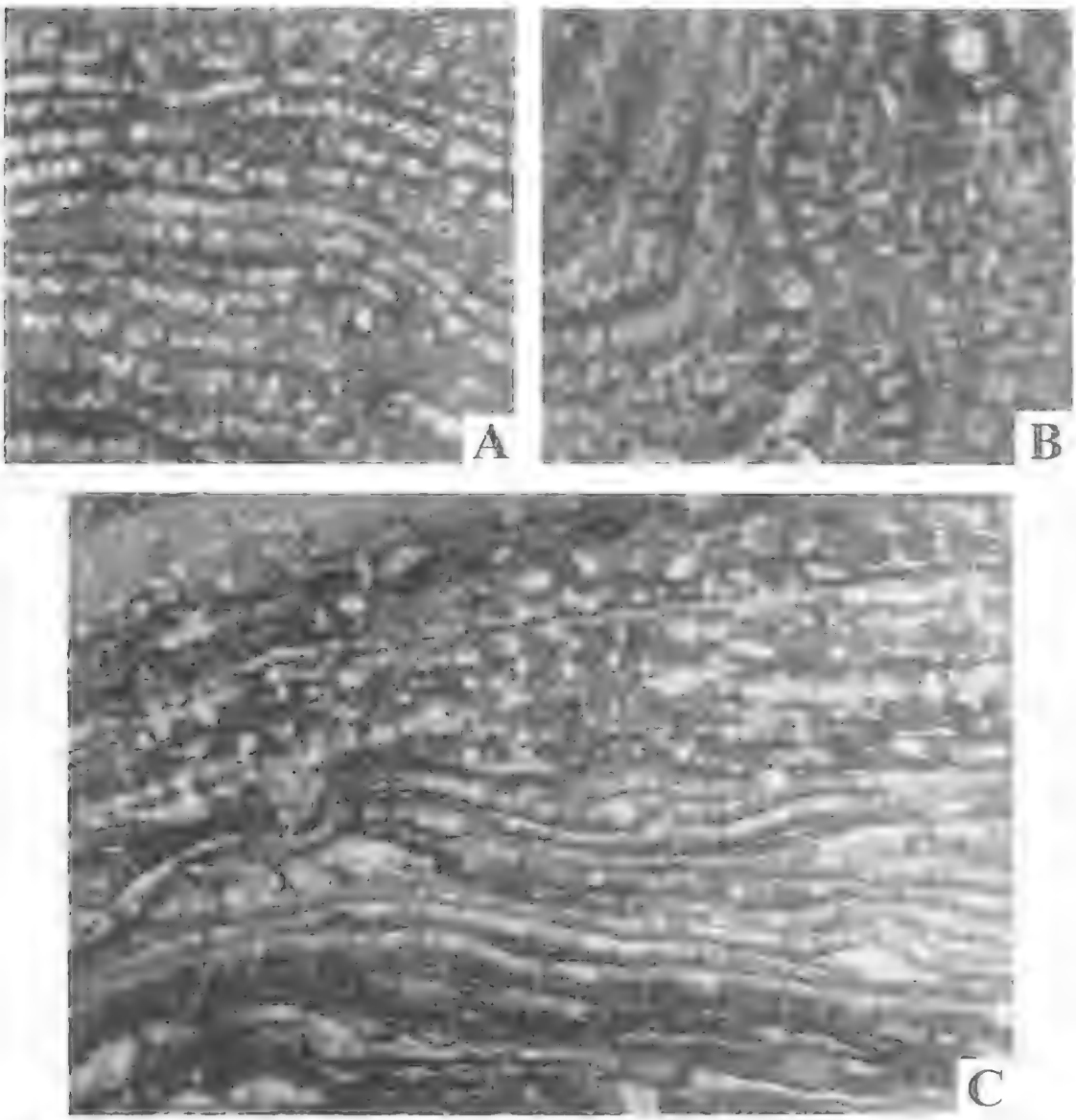



FIG. 28. *Clathrocoilona abeona* Yavorsky 1931 JCUF12750 × 10. A, vertical section; B, tangential section; C, *Clarthrocoilona spissa* (Lecompte, 1951) JCUF11426 × 10, vertical section.

has comparable pillar and laminar spacings, irregular galleries, element thicknesses and astrorhizal development. *C. spissa* (Lecompte) has more occluded galleries and is more solid in tangential section. *C. saginata* (Lecompte) has a finer, more regular grid network, and in tangential section skeletal elements are better differentiated. Fischbuch (1969) placed *Stromatoporella irregularis* Lecompte in synonymy with this taxon. It is viewed here as closer to *C. spissa*, given the more irregular nature of the galleries.

**Clathrocoilona spissa** (Lecompte, 1951)
(Figs 28C, 29)

*Stromatoporella spissa* Lecompte 1951: 187, pl. 37, figs 3-4. Kazmierczak 1971: 92, pl. 21, figs. 2a-b.
*Clathrocoilona* cf. *spissa* (Lecompte), Stearn 1961: 945, pl. 107, figs. 7-8:
*Clathrocoilona spissa* (Lecompte) Zukalová 1971: 56, pl. 15, figs. 1-2: Flügel 1974:. 165, pl. 24, figs. 2,4, pl. 26.

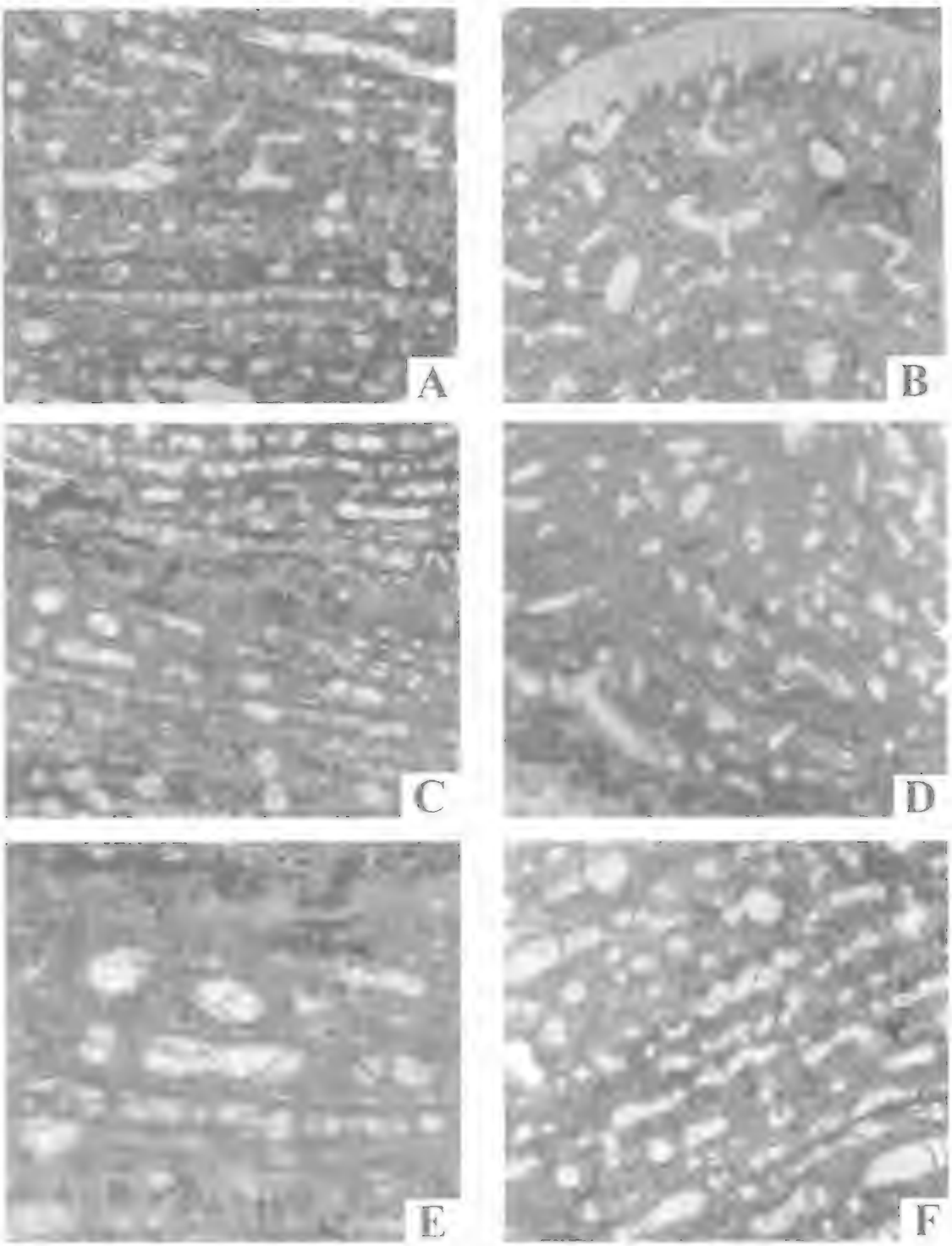



FIG. 29. *Clathrocoilona spisa* (Lecompte, 1951). A, B, JCUF11421. A, vertical section × 10; B, tangential section × 10. C, D, JCUF11432. C, vertical section × 10; D, tangential section × 10. E, F, JCUF11428. E, vertical section × 10; F, tangential section × 10.

fig. 4, pl. 27, fig. 5; Mistiaen 1980: 196, pl.7, figs. 3-9; Cockbain 1984: 25, pl. 11a-d; Mistiaen 1985:. 96, pl. 6, figs. 6-8; Mistiaen 1988: 174, no figs.

*? Clathrocoilona, ? Stromatoporella spissa* Lecompte, Flügel & Flügel-Kahler 1968: 534, p. 399.

MATERIAL. JCUF11413-18, 11420-32, all from JCUL788.

DESCRIPTION. Skeleton thin, laminar, generally encrusting, in general strongly latilaminate. Base of each latilamina has a somewhat ordered array of skeletal elements 1 to 2 laminae thick in which laminae are continuous, commonly with a light median layer, and compact pillars that are spool-shaped and rarely superposed. This gives way to a much thickened amalgamate network in which tissue occupies approximately 70% of the skeleton. Pillars and laminae are difficult to differentiate. Galleries small, rounded or elongated, and 0.1-0.3mm high. They often extend upwards to form 'coenotubes' several laminae high (up to 1mm) or traverse laminae obliquely forming part of astrorhizae. The galleries are commonly crossed by dissepiments. In tangential section skeletal elements dominate, astrorhizal systems are obvious and galleries appear vermicular, up to 0.5mm wide. Microstructure is compact to flocculent.

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Middle Devonian (Givetian);Boulonnais, France, Middle to Late Devonian (Givetian to Frasnian); Dinant Basin, Belgium, Middle to Late Devonian (Givetian to Frasnian); Holy Cross Mountains, Poland, Middle to Late Devonian (Givetian to Frasnian); Afghanistan, Late Devonian (Frasnian); Moravian Karst, Czechoslovakia, Late Devonian (Frasnian); Canning Basin, Western Australia, Late Devonian (Frasnian).

REMARKS. The thickened skeletal elements, the laminae with a median light line, and the diminished galleries are consistent with *Clathrocoilona Yavorsky*, and in particular with *C. spissa* (Lecompte, 1951). *C. spissa* (Lecompte, 1951) differs from other species of *Clathrocoilona* by the density of skeletal architecture, especially in tangential section, the obliteration of galleries, the characteristic latilamination, the vertically elongate galleries and the oblique astrorhizal tubes. Mistiaen (1988) doubted the assignment of Canning Basin material referred by Cockbain (1984) to *C. spissa* (Lecompte, 1951). Mistiaen (1985, 1988) regarded figures 11c and d of Cockbain (1984) as more like *C. obliterata* (Lecompte, 1951). Cockbain's (1984) figures do not relate well to Lecompte's (1951) illustrations of *Stromatoporella obliterata*, and his original identification of the Canning material is supported. Inspection of some of Cockbain's original material has confirmed this view.

## HERMATOSTROMATIDAE
Nestor, 1964

### **Hermatostroma** Nicholson, 1886b

*Hermatostroma* Nicholson 1886b: 105; Lecompte 1952: 247; Yavorsky 1955: 140; Lecompte 1956: F131; Galloway & St Jean 1957; 217: Galloway 1957: 451; Galloway 1960: 635; Stearn 1966a: 106; Stearn 1966b: 59; Birkhead 1967: 78; St. Jean 1967: 424; Flügel & Flügel-Kahler 1968: 547; Fischbuch 1969: 171; Kazmierczak 1971: 122:;Zukalová 1971: 80; Khromych 1974: 41; Flügel 1974: 170; Khromych 1976: 65; Yang & Dong 1979: 67; Mistiaen 1980: 202; Stearn 1980: 842; Stock 1982: 664; Dong 1983: 293; Bogoyavlenskaya & Khromych 1985: 78; Dong 1988: 31; Stock, St. Jean & Otte 1990: 5.

TYPE SPECIES. *Hermatostroma schlueteri* Nicholson, 1886b, by monotypy, from the Middle Devonian of the Paffrath District, Germany.

DISTRIBUTION AND AGE. Widely distributed through the Old world and Eastern Americas Realm late Early to Late Devonian.

REMARKS. The genus *Hermatostroma* Nicholson 1886b, with type species *H. schlueteri*, from the Middle Devonian of Paffrath, Germany, has found considerable usage with a large number of assigned species. A major problem with this genus is the interpretation of its microstructure, and in particular, the conflict between forms with cellular microstructure (melanospheric to some authors) and to those with compact skeletal material and marginal vesicles, cellules and peripheral membranes.

Webby, Stearn & Zhen (1993) have placed Ripper's (1937d) 2 species of *Hermatostroma* within *Pseudotrupetostroma*. *Stromatoporella loomberensis* Dun in Benson (1918) is undoubtedly a *Hermatostroma*, as noted by Flügel & Flügel-Kahler (1968). Cockbain (1984) described *H. ambiguum* Cockbain, *H. perseptatum* Lecompte, *H. roemeri* (Nicholson) and *H. schlueteri* Nicholson from the Canning Basin.

There appears to be a consensus on the higher level systematics of this genus, with most authors reflecting the view that the hermatostromatids are a family level grouping (Bogoyavlenskaya, 1969; Khalfina and Yavorsky, 1971; Stearn, 1980).

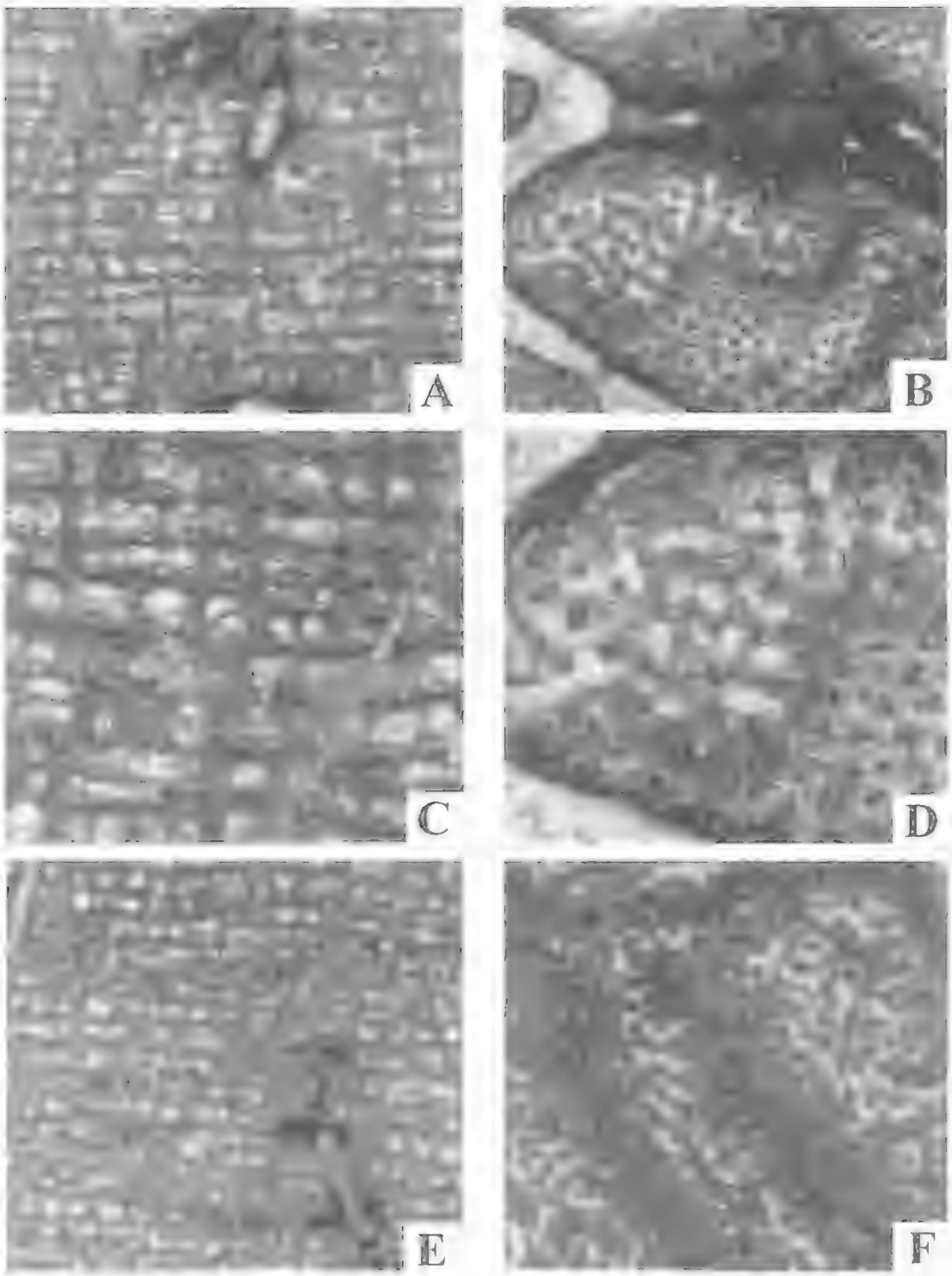



FIG. 30. *Hermatostroma episcopale* Nicholson, 1892. A, D, JCUF11856. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D, tangential section × 20. E, F, JCUF11855. E, tan vertical section × 10; F, tangential section × 10.

**Hermatostroma episcopale** Nicholson, 1892
(Figs 30, 31)

*Hermatostroma episcopale* Nicholson 1892: 219, pl. 28, figs. 4-11; Lecompte 1952: 216, pl. 48, fig. 4, pl. 49, figs. 1-2; Galloway 1960: 635, pl. 77, figs 4a,b; Yang & Dong 1963: 162, pl.10, figs 3-6; Zukalová 1971: 82, pl. 11, figs. 5,6, pl. 27, figs. 1,2; Kazmierczak 1971: 124, pl. 8, fig. 6, pl. 34, figs. 2a,b; Yang & Dong 1979: 68, pl. 32, figs. 7,8; Bogoyavlenskaya & Khromych 1985: 20.

Not *Hermatostroma episcopale* Nicholson, Ripper 1937d:. 29, pl. 5, figs. 7-8.

MATERIAL. JCUF11853-8, 11863-5, 11873 from JCUL787, JCUF11859-62, 11894, 11900 from JCUL794, JCUF11867, 11870, 11890, 11893, 11896, 11899 from JCUL778, JCUF11869, 11872, 11897-8 from JCUL779, JCUF11866, 11868, 11891-2 from JCUL781, JCUF11871 from JCUL793, JCUF11874 from JCUL788, JCUF11895 from JCUL796.

DESCRIPTION. Skeletal shape thick laminar to low domical, maximum width 21cm and maximum height 9cm, not obviously latilaminate. Skeletal elements form a highly regular grid in vertical section. Laminae continuous, gently undulose, 11-18 per 5mm, and 0.05-0.20mm thick with a persistent, thin, dark, compact central line and light margins or well developed peripheral membranes. Pillars continuous, superposed and spool-shaped in interlaminar spaces. Peripheral membranes extend onto pillar margins, but pillars lack the dark central line of the laminae. Pillars spaced 10-15 per 5mm, 0.15-0.28mm thick. Galleries rectangular with rounded margins produced by peripheral membranes or lighter peripheral material on laminae. Abundant arcuate, compact dissepiments. In tangential section, laminar cross sections appear as sweeping bands of diffusely melanospheric skeletal material commonly with a diffuse central dark zone. Where isolated, pillars are rounded to short vermiform in outline, and often joined by dissepiments. Membranes around pillar elements rarely preserved in tangential section where skeletal material often has a melanospheric appearance. No obvious astrorhizae in the specimens.

MORPHOMETRICS.

| Specimen | P5 | Pt | L5 | Lt |
|---|---|---|---|---|
| JCUF11855 | 12.8 (1.0) | 0.20 (0.03) | 15.3 (1.1) | 0.16 (0.05) |
| JCUF11856 | 13.4 (1.2) | 0.15 (0.04) | 13.7 (1.1) | 0.15 (0.03) |
| JCUF11862 | 13.3 (1.8) | 0.16 (0.02) | 13.0 (1.7) | 0.15 (0.04) |
| JCUF11865 | 14.1 (1.6) | 0.19 (0.04) | 12.5 (0.9) | 0.18 (0.05) |
| Average | 13.4 (1.6) | 0.17 (0.04) | 13.6 (1.6) | 0.16 (0.04) |

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Givetian; Devon, U.K., Middle Devonian; Dinant Basin, Belgium, Frasnian; Holy Cross Mountains, Poland, Givetian-Frasnian; Moravian Karst, Czechoslovakia, Givetian-Frasnian; Gueizhou, China, Givetian; Guangxi, China, Givetian; Xizang, China, Frasnian.

REMARKS. The regular grid and peripheral membranes or light margins allies this material to *Hermatostroma*. The pillar-laminar spacing, the abundant dissepiments and the unusual microstructure are inseparable from *H. episcopale*. This species differs from *H. maculatum* by the pillar-laminar spacing, and the abundant dissepiments, and microstructural characteristics. *H. episcopale* has a much more open network than *H. ambiguum* .

**Hermatostroma maculatum**
Yang & Dong, 1979
(Figs 32, 33)

*Hermatostroma maculatum* Yang & Dong 1979: 67, pl. 38, figs 3-4.

MATERIAL. JCUF 11904-11907, 11909, 11910, 11914, ?11921 from JCUL779; JCUF 11908, 11911 - 11913, 11916, 11917, ?, 11923-11925, 11927 and ?, 11918, ?11919, ?11920, ?11926 from JCUL781; JCUF 11915 from JCUL795.

DESCRIPTION. Skeletal shape variable, most commonly low domical or thick laminar. Laminae continuous, gently undulating, 14-22 per 5 mm (mean = 19.1, $\sigma$= 1.9, n= 40); 0.09-0.23 mm thick (mean = 0.16, $\sigma$= 0.03, n= 40), with prominent dark median line, peripheral membranes and light margins or marginal vesicles. Pillars spool-shaped, superposed, 15-23 per 5 mm (mean = 17.4, $\sigma$= 2.2, n= 40), and are 0.08-0.28mm thick (mean = 0.14, $\sigma$= 0.04, n= 40); commonly with lighter margins or peripheral membranes. Galleries rounded due to preponderance of peripheral membranes, generally longer than high, uncommonly crossed by dissepiments. Tissue compact. Astrorhizae 5-7 mm across, with numerous dissepiments in longitudinal section.

MORPHOMETRICS.

| Specimen | P5 | Pt | L5 | Lt |
|---|---|---|---|---|
| JCUF11830 | 16.0 (1.2) | 0.15 (0.05) | 19.8 (1.6) | 0.16 (0.03) |
| JCUF11836 | 19.1 (1.4) | 0.13 (0.01) | 17.6 (0.9) | 0.14 (0.05) |
| JCUF11838 | 18.3 (2.3) | 0.14 (0.03) | 20.1 (1.6) | 0.16 (0.03) |
| JCUF11839 | 16.1 (1.2) | 0.15 (0.03) | 18.7 (2.2) | 0.17 (0.02) |
| Average | 17.4 (0.2) | 0.14 (0.04) | 19.1 (1.9) | 0.16 (0.02) |

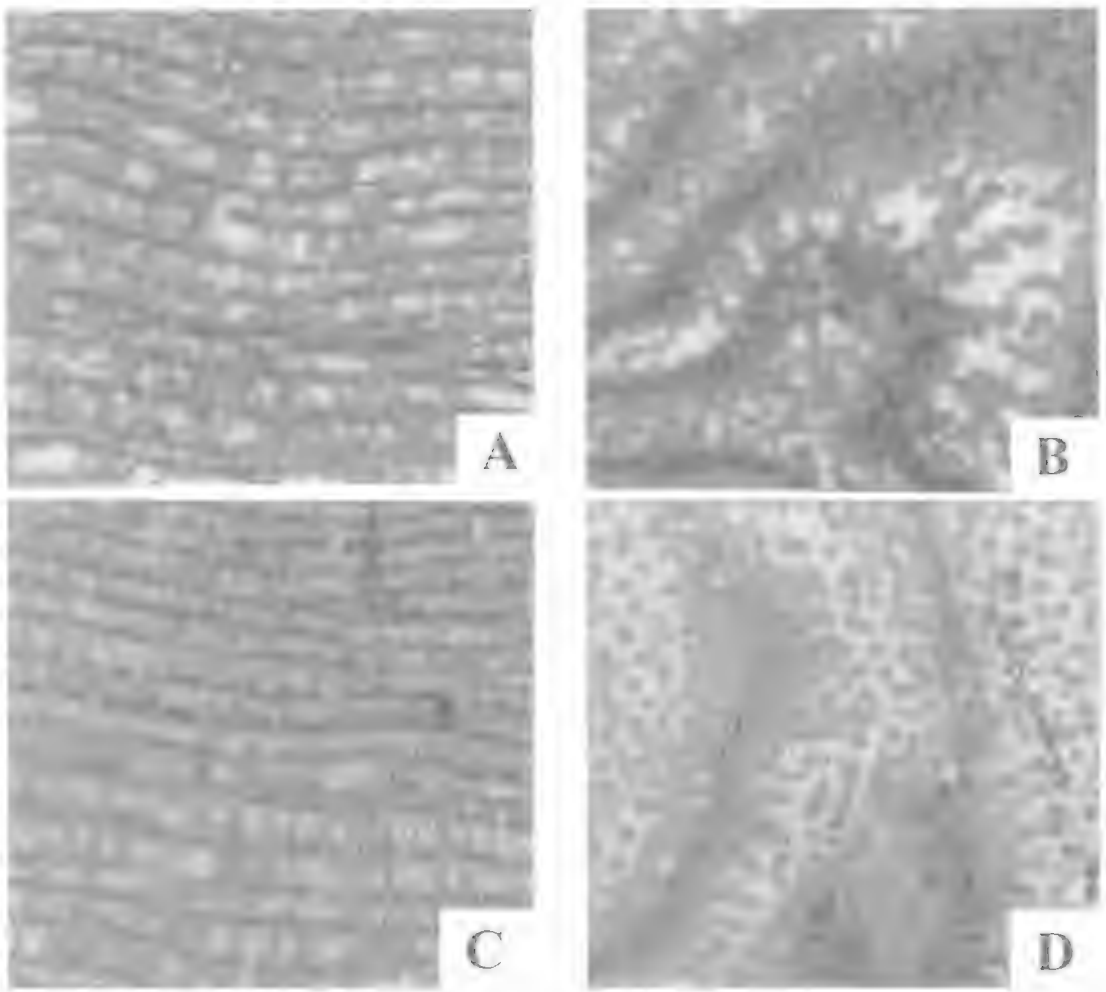



FIG. 31. *Hermatostroma espiscopale* Nicholson, 1892. A, B, JCUF11865 × 10. A, vertical section; B, tangential section. C, D, JCUF11862 × 10. C, vertical section; D, tangential section.

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Givetian; Guangxi, China, Givetian.

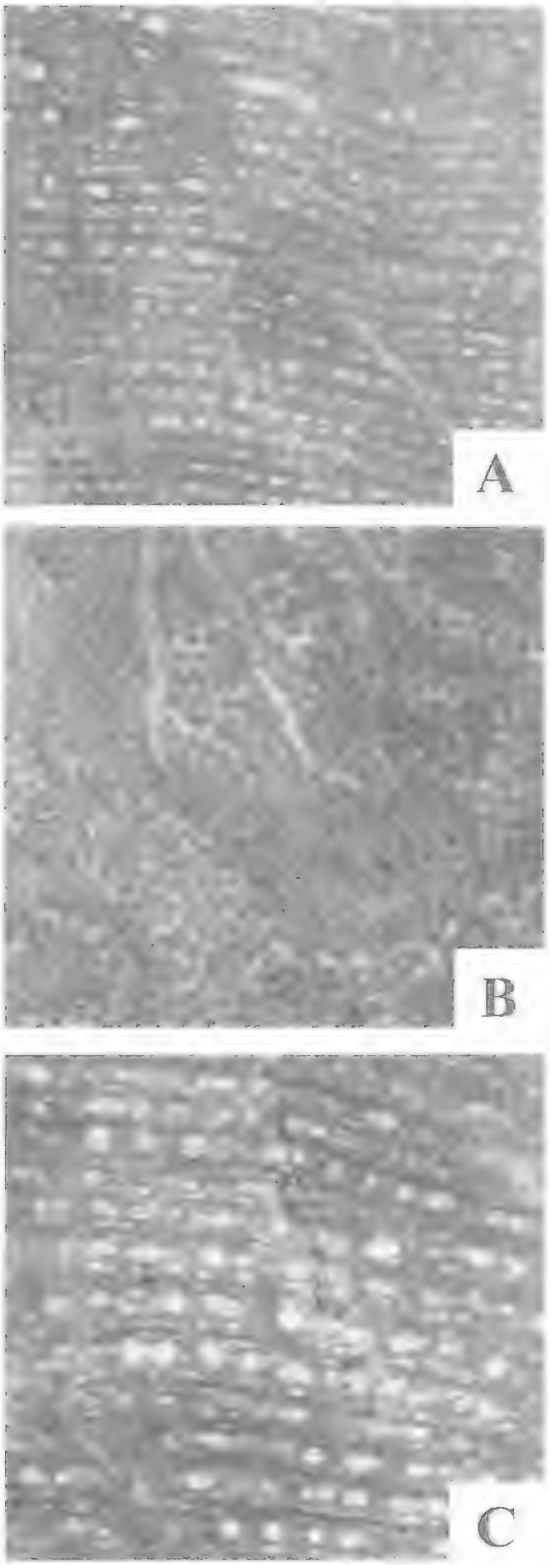
REMARKS. Presence of distinct peripheral membranes, marginal vesicles and light margins in skeletal elements within the same thin section highlights the variable character of the genus. The dominance of membranes places it within *Hermatostroma*. The spacing of skeletal elements and the relative scarcity of dissepiments (compared to other *Hermatostroma* from the Burdekin Formation) identifies the material as conspecific with *H. maculatum* Yang & Dong 1979. It is separated from other Burdekin *Hermatostroma* by the spacing of pillars and laminae and the paucity of dissepiments.

**Trupetostroma** Parks, 1936

*Trupetostroma* Parks 1936: 52: Kuhn 1939 p. A44: LeMaitre 1949: 519:Lecompte 1952: 219: Lecompte 1956: F132: Galloway & St. Jean 1957: 158: Galloway 1957: 439: Khalfina 1960: 342: Khalfina 1960: 59: Galloway 1960: 624: Galloway & Ehlers 1960: 58: Stearn 1962: 3: Stearn 1963: 657: Yavorsky 1963: 66: Stearn 1966a: 102: Stearn 1966b: 49: Birkhead 1967: 60: Flügel & Flügel-Kahler 1968: 580: Zukalová 1971: 74: Kazmierczak 1971: 111: Stearn 1975: 1652: Khromych 1976: 66: Yang & Dong 1979: 40: Stock 1982: 665: Bogoyavlenskaya & Khromych 1985: 92: Stock, St. Jean and Otte 1990: 8.

TYPE SPECIES. *Trupetostroma warreni* Parks, 1936, p. 52, pl. 10, figs. 1-2, by original designation from the Middle Devonian of Slave Lake.

DISTRIBUTION AND AGE. Widely distributed, Early to Late Devonian (Frasnian).




REMARKS. *Trupetostroma* has been well documented by many authors and requires no additional detailed comment. A number of authors have described dendroid members of the genus. These include *Idiostroma mclearni* Stearn (1962) regarded as *Trupetostroma* by Fischbuch (1970b) and Cockbain (1984), and *T. ernoides* and *T. keratodendroides*, described by Fischbuch (1970) from the Swan Hills Formation, Canada.

**Trupetostroma zheni** sp. nov.
(Fig. 34A-E)

ETYMOLOGY. The trivial name is for Zhen Yong Yi who so thoroughly described the rugose corals of the Fanning River Group.

MATERIAL. HOLOTYPE: JCUF11765 from JCUL784. PARATYPES: JCUF11767-11769 from JCUL784; JCUF11766, 11770, 11771 from JCUL778.

DIAGNOSIS. Robustly stachyodiform *Trupetostroma* with regular open macrostructure, concentric thick laminae and spool-shaped, superposed pillars.

DESCRIPTION. Skeleton robustly stachyodiform with branch diameters up to 14mm. Pillars spool-shaped, most commonly superposed, 0.12-0.13mm thick, 6-6.4 per 2mm. Laminae concentrically disposed, continuous and relatively thick (0.11-0.13mm), 7-8.5 per 2mm, sporadically pierced by vacuoles. Tissue compact. Within the axial zone of the skeleton the pillars are short and vermiform. A questionable axial canal is present within each of JCUF11768 (0.1mm), JCUF11769 (0.3mm), and JCUF11765 (0.3mm) but is absent in other specimens.

MORPHOMETRICS. (n=5 for each)

| Specimen | P2 | Pt | L2 | Lt |
|---|---|---|---|---|
| JCUF11768 | 6.2 (1.2) | 0.13 (0.03) | 8.0 (0.9) | 0.13 (0.03) |
| JCUF11769 | 6.0 (0.9) | 0.12 (0.02) | 8.4 (0.5) | 0.13 (0.03) |
| JCUF11765 | 6.4 (0.5) | 0.14 (0.03) | 7.2 (1.0) | 0.12 (0.03) |

DISTRIBUTION AND AGE. Burdekin Formation, north Queensland, Middle Devonian, Givetian.

REMARKS. Reference to *Trupetostroma* is indicated by the presence of a light axial zone within the laminae and conspicuously spool-shaped pillars, and is reinforced by the

FIG. 32. *Hermatostroma maculatum* Yang & Dong, 1979. JCUF11838. A, vertical section × 10; B, tangential section x 10; C, vertical section × 20.

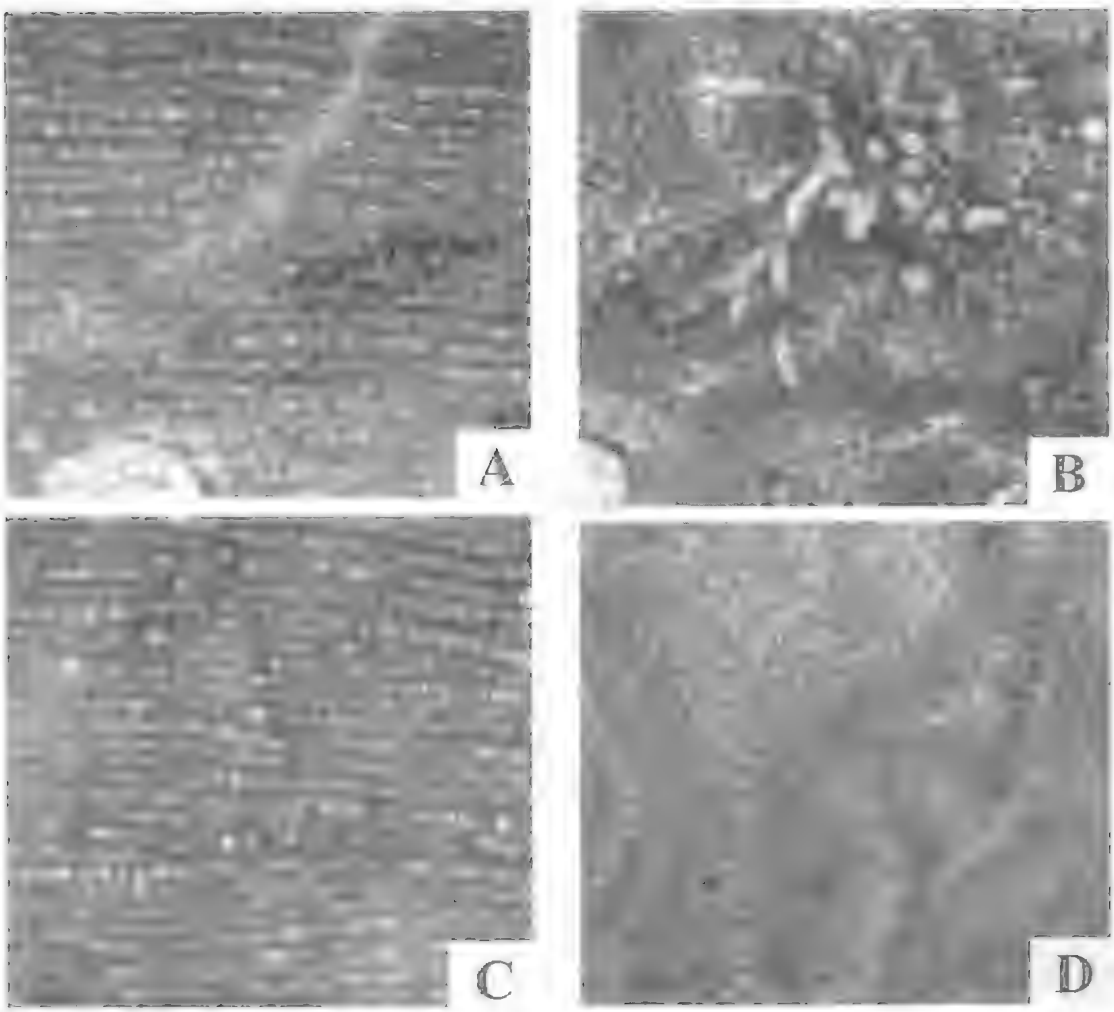



FIG. 33. *Hermatostroma maculatum* Yang & Dong, 1979. A, B, JCUF11832. A, vertical section × 10; B, tangential section × 10. C, D, JCUF11830. C, vertical section × 10; D, tangential section × 10.

presence of poorly developed vacuoles in JCUF11768. This species differs from most other species of *Trupetostroma* in its characteristically robustly dendroid skeleton. *T. mclearni* (Stearn, 1962) possesses a better developed axial canal, and the skeletal architecture is not as well differentiated. *T. ernodes* Fischbuch has a wide, disordered axial zone, missing in this taxon. *T. keratodendroides* Fischbuch has a prominent axial canal and thicker pillars.

The specimens are broadly comparable with *Hermatostroma roemeri* (Nicholson) but this species has a much more prominent axial canal and clearly developed marginal vesicles. They superficially resemble *Idiostroma* aff. *uralicum* Yavorsky but this species has much shorter pillars which are not as well superposed and is much smaller. The former characteristic was that used by Zukalová (1971) to place *Idiostroma* aff. *uralicum* within *Dendrostroma*. *Dendrostroma oculatum* (Nicholson) grossly resembles *T. zheni* but lacks superposed pillars.

AMPHIPORIDA Ruhkin, 1938
AMPHIPORIDAE Rukhin, 1938

**Amphipora** Schulz, 1883

*Amphipora* Schulz 1883, p. 89. (not seen); Nicholson 1886b: 109; Etheridge 1917: 239; Chi 1940: 312; Lecompte 1952: 321; Yavorsky 1955: 149; Gogolczyk 1956: 211; Lecompte 1956: F142; Galloway 1957: 442; Galloway & Ehlers 1960: 97; Stearn 1966: 109; Birkhead 1967: 83; Fischbuch 1970a: 68; Zukalová

1971: 10; Stearn 1980: 831; Stock 1982: 660; Stock, St. Jean & Otte 1990: 2. Stearn, 1997:833.
*Paramphipora* Yavorsky 1955: 154.
*Haraamphipora* Rukhin 1938: 93.
Not *Amphipora* Schulz, Ripper 1937a: 37.

TYPE SPECIES. *Caunopora ramosa* Phillips, 1841 from the Middle Devonian of Chudleigh, Devon, England by monotypy.

DISTRIBUTION. Widely distributed, Emsian to Famennian.

REMARKS. Stearn (1997) reviewed the concept of the genus and type species and provides a full generic synonymy.

### **Amphipora ramosa** (Phillips, 1841) (Fig. 35A-H)

*Caunopora ramosa* Phillips 1841: 19, pl. 8, fig. 22.
*Amphipora ramosa* (Phillips), Schulz 1883: 246, pl. 22, fig. 5-6 pl. 23, fig. 1; Nicholson 1886b: 109, 223, pl. 9, fig. 1-4. pl. 29, fig. 3-5; Felix 1905: 73, fig. 1-3; Riabinin 1931: 508, pl. 1, figs. 11-13, fig. 1; Chi 1940: 312, pl. 5, fig. 1-4.Yu 1947; 125 pl. 1, fig. 2a,b: Lecompte 1952: 325, pl. 67, fig. 3. pl. 68., fig. 1-3; Fontaine 1955: 57, pl. 1, fig. 1-4; Yavorsky 1955: 152, pl. 82, fig. 1-4, pl. 84, fig. 2-3; Gogoloczyk 1956: 224 pl. 2, fig. 1-4, text fig. 2-4; Galloway & St Jean 1957: 233, pl. 23, fig. 2-6; Yavorsky 1957: 63, pl.41, fig. 1-9; Galloway & Ehlers 1960: 98, pl. 11, fig. 1a,b; Yavorsky 1961: 68, pl. 38, fig. 15, pl. 37, figs 1-10; Stearn 1961: 946, pl. 107, figs 9,10; Stearn 1963: 663, pl. 87, fig. 2; Stearn 1966: 63, pl. 24, fig. 2; Flügel & Flügel-Kahler 1968: 342;Fischbuch 1970: 69, pl. 15, figs. 1-5; Stearn & Mehrotra 1970: 19, pl. 4, fig. 2; Khromych 1971: 133, pl. 36, fig. 7; Zukalová 1971: 117, pl. 37, fig. 1, pl. 38, fig. 1-4, pl. 40, fig. 2; Stearn 1975: 1665; Yang & Dong 1979: 79, pl. 43, figs. 7,8; Bogoyavlenskaya & Khromych 1985: 48; Khromych & Hung 1988: 31, pl 14, figs. 5-6. Stearn 1997: 845, figs 1-11.
*Amphipora ramosa* (Phillips). *minor* Riabinin, Khromych 1976: 74, pl. 14,fig. 3; Wang & Huang, 1985: 411,pl. 2, figs 3,4.
*Amphipora ramosa* (?)(Phillips), Fagerstrom 1982p. 35, pl. 6, fig. 5,6,9; Dong & Wang 1982: 26, pl. 16, figs. 6-9.
Not *Amphipora ramosa* (Phillips), Ripper 1937a: 38, pl. 1, pl. 1-3.

MATERIAL. JCUF11467, 11469-75, all from JCUL788.

DISTRIBUTION AND AGE. Worldwide, ?Early Devonian, Middle Devonian (particluarly Givetian) to Frasnian.

DESCRIPTION. Dendroid (amphiporiform) skeletons 5-10cm long, 1.7-4.3mm in diameter (mean = 3.1 mm, $\sigma$= 0.5 , n= 105 ) canaliculate or non-canaliculate, axial canal 0.2-0.7mm in diameter (mean = 0.4 mm, $\sigma$= 0.1, n= 65 ). Prominent marginal vesicles sporadically crossed by thin dissepiments. Axial canal generally less than one-quarter of skeletal diameter, commonly crossed by thin dissepiments. Microstructure is fibrous from a dark central line within the centre of the skeleton, and fibrous without the dark central line in peripheral skeletal elements.

MORPHOMETRICS. Skeletal diameters and, where possible, axial canal diameters were measured from thin sections. Minimum diameters were taken for slightly oblique sections. All thin sections show multiple skeletons. A summary of data from the material is presented below, the relationships of canal diameter to branch diameter are shown in Figs 36 and 37.

| Specimen | D mean | Dσ | n | A mean | Aσ | n | % canal |
|---|---|---|---|---|---|---|---|
| JCUF11467 | 2.9 | 0.4 | 16 | 0.35 | 0.06 | 8 | 50 |
| JCUF11469 | 3.3 | 0.4 | 7 | 0.47 | 0.13 | 5 | 71 |
| JCUF11470 | 2.7 | 0.2 | 7 | 0.38 | 0.07 | 6 | 86 |
| JCUF11471 | 3.2 | 0.5 | 6 | 0.46 | 0.14 | 5 | 81 |
| JCUF11472 | 2.9 | 0.5 | 27 | 0.36 | 0.10 | 11 | 41 |
| JCUF11473 | 3.4 | 0.4 | 15 | 0.42 | 0.08 | 12 | 80 |
| JCUF11474 | 3.4 | 0.4 | 14 | 0.38 | 0.08 | 9 | 64 |

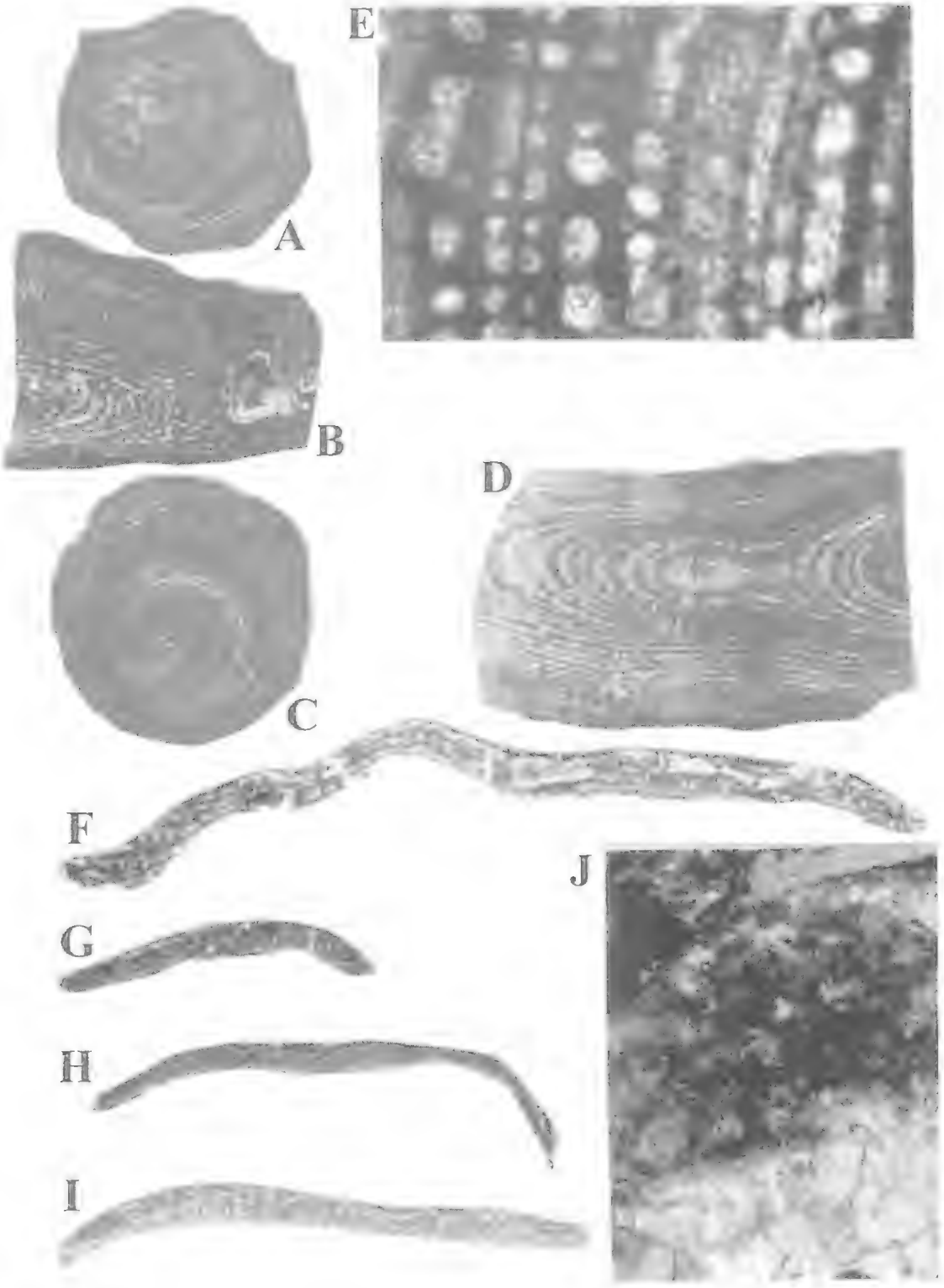
REMARKS. The material is indistiguishable from *A. pervesiculata* Lecompte in skeletal organisation and size. *S. rudis* (Lecompte) is comparable but is distinguished by its greater size and radiating skeletal elements. *Paramphipora mangkamensis* Dong, *P. zhougedongensis* Dong and *Amphipora tenuissina* Dong & Wang are of comparable size and cannot be effectively discriminated from *A. pervesiculata*. *P. mangkamensis* of Dong (1981) seems to lack the large marginal vesicles of *A. pervesiculata*, but this distinction requires confirmation. *P. zhougedongensis* Dong has small marginal vesicles and may be conspecific with *A. pervesiculata*. *Amphipora tenuissina* Dong & Wang resembles, and may be synonymous with *A. pervesiculata*.

Although *A. fidelis* Yavorsky of Dong & Wang (1984) shows some smaller marginal vesicles its size and large axial canal strongly suggests that it is conspecific with *A. pervesiculata* Lecompte.

### **Euryamphipora** Klovan, 1966

*Euryamphipora* Klovan 1966: 14; Flügel & Flügel-Kahler 1968: 544; Fischbuch 1970a: 72; Stearn 1980: 891; Mistiaen 1985: 206; Dong 1988: 32; Stock, St. Jean & Otte 1990: 4.

TYPE SPECIES. *Euryamphipora platyformis* Klovan, 1966 p. 15, pl. 3, figs 4a,b, pl. 4, figs. 1-7, by original designation, from the Frasnian Cooking Lake equivalent of the Leduc Formation, Alberta.


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DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia Givetian; Canada, Givetian-Frasnian; Afghanistan, Givetian-Frasnian; Ferques-Boulonnais, France, Frasnian.

REMARKS. *Euryamphipora*, based on *E. platyformis* Klovan, is a little studied and poorly understood genus. *E. mollis* Fischbuch, 1970a, the only other included species, shows a much more delicate structure, more dissepiments and larger marginal vesicles. Cockbain (1984) synonymised *Euryamphipora* with *Amphipora*, regarding it as a laterally compressed *Amphipora*. However the illustrations of Fischbuch (1970a) and Mistiaen (1988) show an obvious platey form. Specimens from the Burdekin Formation are undulose in nature, and quite distinct from associated *Amphipora*. Hence Cockbain's view is rejected.

**Euryamphipora merlini** sp. nov.
(Fig. 34F-J)

ETYMOLOGY. For Robert Merlin Carter, Professor of Geology, James Cook University of North Queensland.

MATERIAL. Holotype; JCUF11449 from JCUL778, paratypes; JCUF11436, 11438-48 from JCUL778, 780 and JCUF11843-45 from JCUL787.

DIAGNOSIS. Euryamphipora with relatively thick skeletal elements and only moderately inflated upper and lower vesicles.

DESCRIPTION. Skeletal shape thin, laminar, and undulose in encrusting style, 0.7-1.3mm thick, containing only 2 to 5 laminae. Uppermost and lowermost skeletal layer has inflated galleries (vesicles) that are slightly larger than those at the centre of the skeleton. Vesicles 0.1-0.3 mm high. Pillars (0.08-0.12mm) slightly thinner than laminae (0.10-0.14mm) Microstructure transversely fibrous. No dissepiments sighted.

MORPHOMETRICS.

| Specimen | Thickness (mm). |
|---|---|
| JCUF11429 | 1.3 |
| JCUF11439 | 0.7, 0.7 |
| JCUF11443 | 0.7, 0.8, 0.9 |
| JCUF11444 | 1.2, 0.9, 0.7 |
| JCUF11447 | 1.3 |
| Average | 0.92mm (n=10 σ=0.24) |

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Givetian.

REMARKS. The Burdekin specimens differ from *E. platyformis* Klovan, 1966 and *E. mollis* Fischbuch, 1970a in the size of the vesicles, and somewhat thicker skeletal elements. Both *E. platyformis* and *E. mollis* have dissepiments whereas none were found within the Burdekin specimens. No obvious median line within the pillars or laminae has been recognised in *E. merlini*, but the transversely fibrous microstructure is easily recognisable in the holotype and a number of the less altered paratypes. Diagenetic chalcedony has replaced a few of the specimens, and varying degrees of recrystallisation are represented in the suite.

STROMATOPORIDA Stearn, 1980

**Stromatopora** Goldfuss,1826

*Stromatopora* Goldfuss 1826: 21 (not sighted); Winchell 1867: 99; Nicholson 1874: 4; Nicholson 1875: 245; Nicholson & Murie 1878: 217; Bargatzky 1881a: 281; Lecompte 1952: 263; Lecompte 1956: F133; Fritz & Waines 1956: 98; Galloway & Ehlers 1960: 50; Galloway 1960: 627; Flügel & Flügel-Kahler 1968: 568; Khalfina & Yavorsky 1973: 150 (transl.); Stock 1979: 336; Mistiaen 1980: 208; Goldfuss, Stearn: 892; Bogoyavlenskaya & Khromych 1985: 90; Mistiaen 1985: 134; Stearn 1990: 506; Stock, St. Jean, & Otte 1990: 8; Stearn 1993: 210; Webby & Zhen 1993: 344.

? *Stromatopora* Goldfuss, Birkhead 1967: 68.

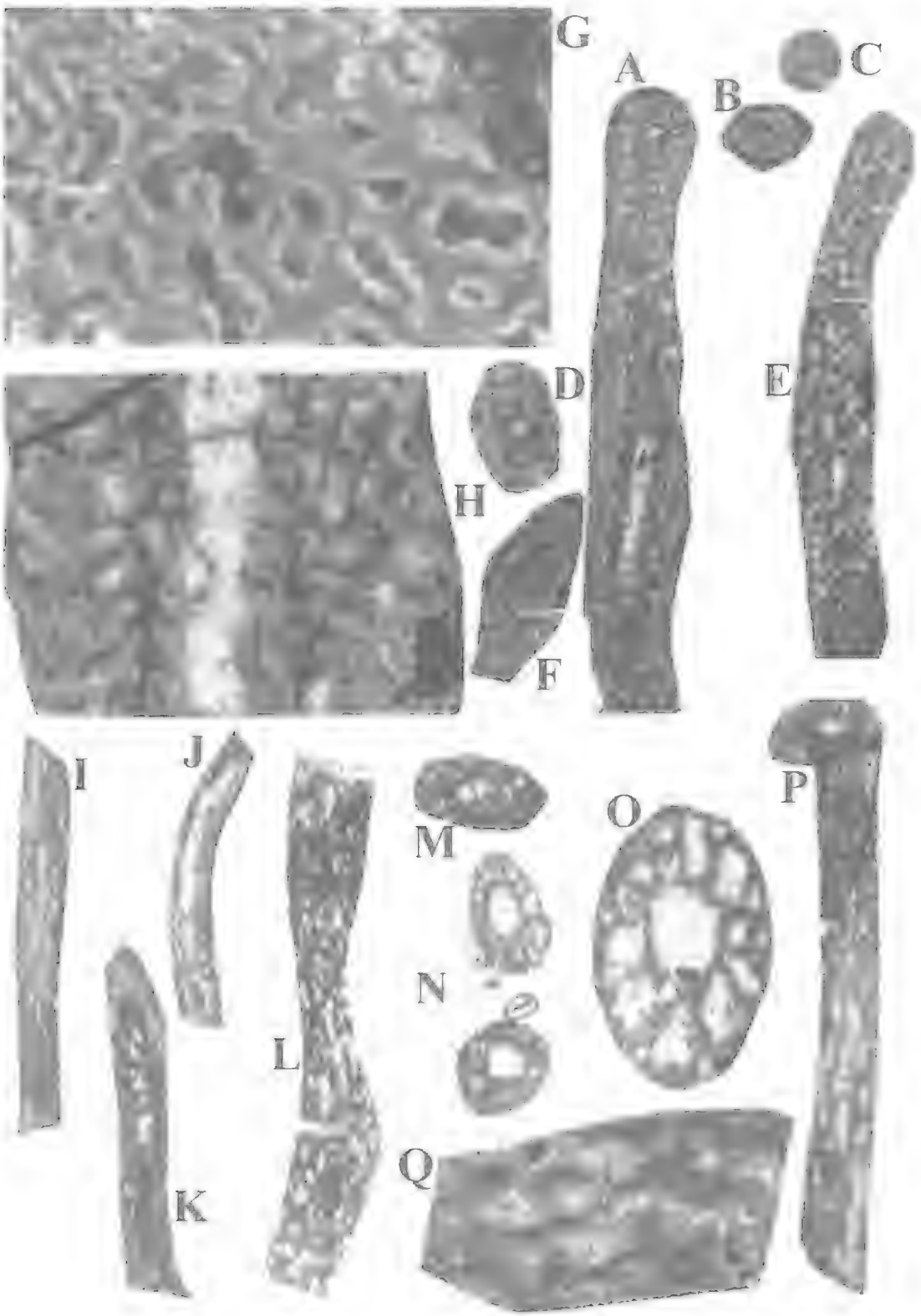
Not *Stromatopora* Goldfuss, Nicholson 1886b: 23; Galloway & St Jean 1957; 164; Galloway 1957: 447; Stearn 1966a: 110; Stock 1984:778.

TYPE SPECIES. *Stromatopora concentrica* Goldfuss by monotypy, from the Middle Devonian of Gerolstein, Germany.

DISTRIBUTION AND AGE. Widely distibuted, Middle Silurian (Wenlock) to Late Devonian (Famennian) (Stearn 1993).

REMARKS. The genus has been recently reviewed by Stearn (1993) and lengthy discussion is unwarranted. Stearn (1993), following Lecompte (1952) and Mistiaen (1985) stressed the original concept of a cassiculate dominant structure in deference to Nicholson (1886b) who emphasised vertical elements in his concept of the genus. The genus has been distilled by Stearn's (1993) reassessment and now carries

FIG. 34. A-E. *Trupetostroma zheni* sp. nov. A, holotype, JCUF11768, transverse section, × 3; B., holotype, longitudinal section, × 3; C, paratype, JCUF11765 transverse section, × 3; D paratype, JCUF11765, transverse section, × 3; E, holotype, transverse section, × 12. F-J, *Euryamphipora merlini* sp. nov., all longitudinal sections. F, holotype, JCUF11449, × 5; G, JCUF11436, × 5; H, paratype, F11445(a), × 5; I, paratype, JCUF11445(b); J, holotype, JCUF11449, × 30.


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only 26 species, plus 8 doubtful species as opposed to the more than 200 assigned by various authors (cf. Flügel & Flügel-Kahler, 1968; Bogoyavlenskaya & Khromych, 1985). The synonymy list is not exhaustive. Stearn (1993) has provided an extensive synonymy.

**Stromatopora huepschii** (Bargatzky, 1881a) (Fig. 40)

*Caunopora hüpschii* Bargatzky1881a: 62.

*Stromatopora hüpschii* (Bargatzky), Nicholson1886b: 26, 92, text fig. 6A,B, pl. 10, figs. 8,9; Nicholson 1891: 176, text fig. 20A, B,pl. 10, figs. 8,9, pl. 22, figs. 3-7; Lecompte 1952: 268, pl. 52, figs. 1-3; Yavorsky 1955: 106, pl. 56, figs, 3-4; Galloway & St. Jean 1957: 168; Galloway 1957: 448, pl. 35, fig. 2; Yavorsky 1961,: 43, pl. 26, figs.4,5; Flügel & Flügel-Kahler 1968: 570; Fischbuch 1969,: 174, pl. 6, figs. 1-5; Yang & Dong 1979: 52, pl. 22, figs. 7,8; Mistiaen 1980: 209, pl. 13, figs. 3-6: Dong & Wang 1982: 52, 19, pl. 10, figs. 5-6; Bogoyavlenskaya & Khromych 1985: 26; Mistiaen 1985: 139, pl. 12, figs. 1-6; Liu & Dong 1991: 318, pl. 2, figs. 4a,b; Dong & Song 1992: 30, pl. 3, figs. 1a,b.

? *Stromatopora alaica* Riabinin 1931: 506, pl. 1, figs. 7,8.

? *Stromatopora sp* cf. *S. huepschii* (Bargatzky), St Jean 1967: 422, pl 1, figs 1-4.

Not *Stromatopora* aff. *S. hüpschii* (Bargatzky), Ripper 1937b: 86, pl. 8, figs. 7,8; Ripper 1937d: 28, pl. 5, figs. 5,6.

MATERIAL. JCUF11772, 11775, 11779, 11780, 11784-6, 11791, 11797-8, 11800-1, 11805, 11928, and 11933 from JCUL788; JCUF11790, 11901, 11929-30 from JCUL787; JCUF11799, 11802-3, and 11902 from JCUL778; JCUF11931 from JCUL794.

DESCRIPTION. Skeletal shape low to medium domical, up to approximately 7cm high and 12cm wide; obscurely latilaminate with latilaminae 0.2-2.5cm thick. Growth surfaces gently to strongly undulose, no obvious mamelons present. In vertical section the structure is a coarse amalgamate network with coenosteles slightly more dominant. Coenosteles short to moderately long, spanning up to 5 coenostromes but mostly less, dominantly erect but a few are oblique, spaced 13-16 per 5mm; very thick, 0.20-0.32mm. Coenostromes of variable length, generally oblique, sporadically persistent along bases of latilaminae, locally replaced by dissepiments. Coenostromes irregularly spaced, making measurement of spacing impossible, a little thinner (0.15-0.22mm) than coenosteles. Galleries irregular with rounded margins, either vertically lengthened, horizontally elongate or an irregular combination of both, are most commonly crossed by relatively flat dissepiments. Both vertical and horizontal elements coarsely cellular where well preserved, but dissepiments appear compact. In tangential section coenosteles form a labyrinthine network in which galleries range from small and rounded in cross-section to long, irregular and vermiform. No obvious traces of astrorhizae, but sporadically the gallery traces complexly radiate from a central zone, suggesting a diffuse system. Syringoporid symbionts are common in this taxon.

DISTRIBUTION. Germany, Middle Devonian; Spain, Middle Devonian; Italy, Middle Devonian; England, Middle Devonian; France, Givetian; Belgium, Givetian to Frasnian; Kuznetz Basin, Russia, Givetian; Yunnan, China, Givetian; Guangxi, China, Givetian; Xinshau, China, Givetian; Afghanistan, Emsian to Givetian; Alberta, Canada, Givetian; California, United States, undiff. Devonian; Burdekin Subprovince, north Queensland, Australia, Givetian.

REMARKS. Well preserved specimens are indistiguishable from *S. huepschii* (Bargatzky) as figured by a number of authors including Nicholson (1886b), Lecompte (1952), and Galloway (1957). Lecompte (1952, pl. 52, fig 2,2a,b) figured the type specimen, and although there is dominance of vertical elements in some of the sections and moderate occlusion of the galleries in tangential section, there is sufficient development of a cassiculate network to warrant inclusion in *Stromatopora*. The moderate development of coenostromes precludes assignment to *Salairella*. Material assigned to this species by Ripper (1937b,d) has been reassigned to *Syringostromella zintchenkovi* (Khalfina) and to *Syringostromella* cf. *labyrinthia* Stearn by Webby, Stearn & Zhen (1993).

FIG. 35. A-H, *Amphipora ramosa* (Phillips, 1841). A, JCUF11469, longitudinal section, × 5; B, JCUF11472, transverse section, × 3; C, JCUF11475 transverse section, × 3; D, JCUF11769, transverse section, × 3; E, JCUF11475, longitudinal section, × 3; F, JCUF11469, transverse section (oblique), × 3; G, JCUF11475, transverse section, × 30; H, JCUF11469, longitudinal section, × 25. I-Q, *Amphipora pervesiculata* Lecompte, 1952; I, JCUF11460, longitudinal section, × 5; J, JCUF11461, longitudinal section, × 5; K, JCUF11460, longitudinal section, × 5; L, JCUF11447, longitudinal section, × 5; M, JCUF11460, transverse section, × 5; N, JCUF11447, transverse section, × 5; O, JCUF11462, transverse section, × 16; P, JCUF11460, longitudinal section and transverse section, × 7; Q, JCUF11447, longitudinal section, × 15.

**Stromatopora** sp.
(Fig. 41)

MATERIAL. JCUF12025-28, 12054-6, 12058. All are from JCUL788.

DESCRIPTION. Medium domical skeleton up to 10cm wide and 6cm high; terminal surface not preserved, but strongly undulating coenostromes suggest well developed mamelons. Skeleton with crude latilaminae 5-15mm apart. Astrorhizae poorly preserved. In vertical section skeletal network variable, ranging from a cassiculate network to zones where vertical elements are more prominent. Coenosteles relatively short, commonly oblique, but where longer persist for up to 3 coenostromes high, 7-8 per 2mm, relatively thin (0.05-0.10mm) and coarsely cellular or melanospheric. Coenostromes shorter, impersistent, more often oblique, forming a classic cassiculate network, 6-8 per 2mm and 0.05-0.10mm thick. Galleries rounded or slightly higher than wide. Rare, gently arcuate dissepiments cross the higher galleries. In tangential section galleries rounded to shortly vermiform, and the skeletal structure is relatively closed. In both LS and TS common, much thicker astrorhizal canals are present. They are irregular and suggest a complex, large canal system. No dissepiments preserved in these canals.

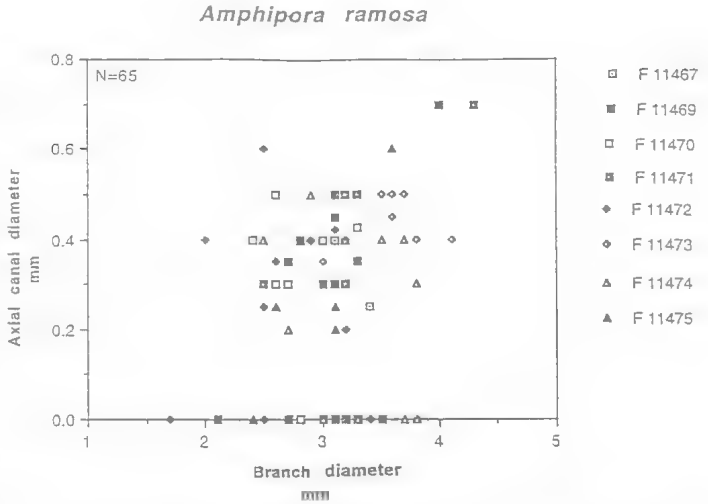



FIG. 36. Branch diameter plotted against axial canal diameter for *Amphipora ramosa* (Phillips, 1841) from the Burdekin Formation.

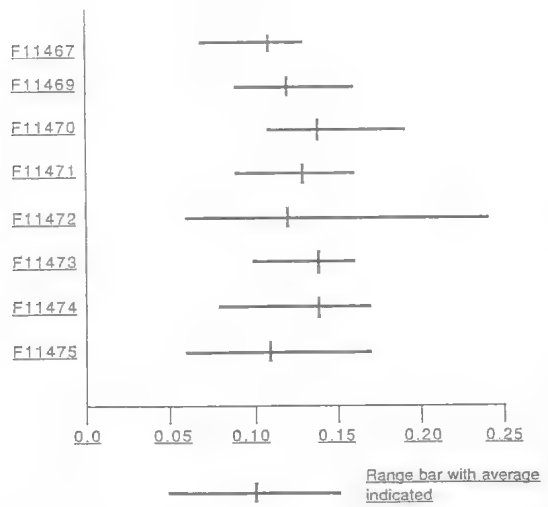



FIG. 37. Ratio of axial canal diameter to branch diameter for *Amphipora ramosa* (Phillips, 1841) from the Burdekin Formation.

REMARKS. The material is confidently assigned to *Stromatopora* on the basis of the cellular skeletal elements which form a cassiculate network. It differs from Burdekin *S. huepschii* by the finer skeletal network, and thinner elements. Burdekin material assigned to *Salairella* cf. *S. cooperi* has a much more closed and slightly more ordered skeletal network. Limited material prevents specific assignment.

**Ferestromatopora** Yavorsky, 1955

*Ferestromatopora* Yavorsky 1955,: 109; Galloway 1957: 446; Stearn 1966a: 111; Stearn 1980: 892; Bogoyavlenskaya & Khromych 1985: 76; Stock, St. Jean & Otte 1990: 4; Stearn 1993: 212.

Not *Ferestromatopora* Yavorsky , Galloway1960: 627; Stearn 1966b: 57; Birkhead 1967: 66; Khromych 1976: 63.

In part *Ferestromatopora* Yavorsky , Fischbuch 1969: 175; Kazmierczak 1971: 96; Khromych 1974: 52; Yang & Dong 1979: 56.

TYPE SPECIES. *Ferestromatopora krupennikovi* Yavorsky 1955 from the Middle Devonian of the Kuznets Basin, Tyrgan region, Russia by subsequent designation of Galloway (1957: 446) being the first species described.

DISTRIBUTION AND AGE. Australia, Givetian; Russia Givetian; Poland, Givetian; Canada, Frasnian; China, Givetian.

REMARKS. In a recent review Stearn (1993) has narrowed the generic concept considerably to 4,

or possibly 5 species. Further comment is unnecessary.

**Ferestromatopora heideckeri**
sp. nov.
(Figs 42, 43).

ETYMOLOGY. For Dr E.J. Heidecker, University of Queensland, Brisbane Australia, for his contributions to palaeontologic and other studies of the Burdekin Subprovince.

MATERIAL. HOLOTYPE: JCUF-11983. PARATYPES: JCUF11986, 89, 93. Additional material 11984-12002, 12022 (less holotype and paratype specimens). All from JCUL788.

DIAGNOSIS. *Ferestromatopora* with paralaminae spaced 0.3mm to 2.2m apart, separating a network of sub-vertically oblique thin skeletal elements (coenosteles) 0.05-0.10mm thick, spaced 7-11 in 2mm and somewhat subordinate sub-horizontally oblique elements spaced 8-12 per 2mm, which are 0.05-0.10mm thick.

DESCRIPTION. Skeletal shape medium domical, up to 8.5cm high and 12.0cm wide; mostly known from fragmental material. Latilaminae (paralaminae sets) seen in only thin section. Growth surfaces gently undulose to flat without obvious mamelons or prominent astrorhizae. In vertical section the skeleton is dominated by skeletal network sets separated by continuous, thin compact, laminae or paralaminae (*sensu* Stearn, 1993). The spacing of the paralaminae varies from 0.3mm (1-2 coenostroms) to 2.2mm (7-13 coenostroms) in thickness. Between these laminae thin skeletal elements form a disordered network. Elements short, mostly oblique but dominated by those oriented sub-vertically rather than sub-horizontally. These sub-vertical coenosteles are spaced 7-11 per 2mm and are 0.05 to 0.10mm thick. Sub-horizontal elements (coenostroms) are generally a little shorter, spaced 8-12 per 2mm and are also 0.05-0.10mm thick. They appear subordinate to the sub-vertical elements. Galleries small, mostly rounded and slightly vertically elongate, but they do not extend vertically beyond one coenostrom in thickness. Dissepiments are rare. In tangential section the skeletal elements form an enclosed to labyrinthine structure with galleries vermiform, ovoid or rounded. The microstructure of the skeleton is not well preserved.

In some parts of vertical section, elements which are diffusely melanospheric with fine-grained dark spots are locally adjacent to elements which appear extremely coarsely melanospheric with one or 2 dark spots per element. The laminae are exclusively compact. In tangential section there is sporadic weak development of astrorhizae, consisting of simple, short, walled, and unbranched canals without dissepiments.

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Middle Devonian.




FIG. 38. Branch diameter plotted against axial canal diameter for *Amphipora pervesiculata* Lecompte, 1952 from the Burdekin Formation.

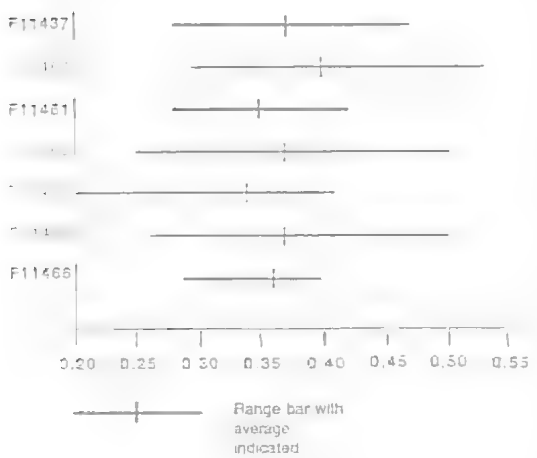



FIG. 39. Ratio of axial canal diameter to branch diameter for *Amphipora pervesiculata* Lecompte, 1952 from the Burdekin Formation.

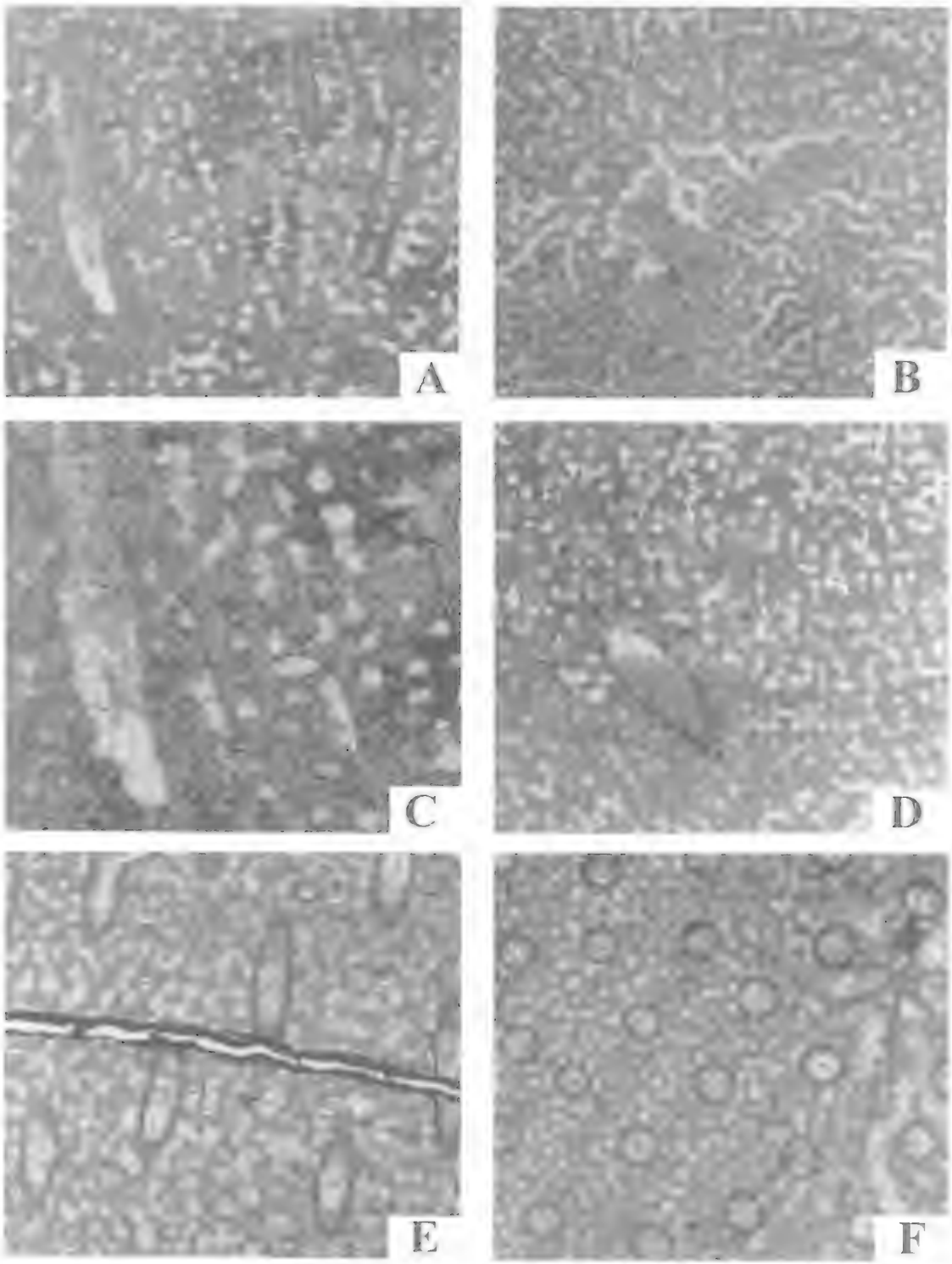



FIG. 40. *Stromatopora hispida* (Bargatzky, 1881a). A-C, JCUF11722. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20. D, JCUF11755 vertical section × 10. E, F, JCUF11931. E, vertical section × 10; F, tangential section × 10.

REMARKS. Paralaminae separating the network packages of oblique elements and, the absence of coenotubes place this material within the generic concept as recently reviewed by Stearn (1993). Yavorksy's (1955) illustrations of the type species *F. krupennikovi* Yavorsky, show somewhat more regularly spaced paralaminae and the network elements are less vertical in aspect. *F. talovensis* Yavorsky has closer-spaced laminae and more reclined elements. *F. tyrganensis* Yavorsky has thicker and obviously more reclined network elements. *F. formosa* Yang & Dong has more closely spaced paralaminae, and thicker interlaminar elements. This new taxon is differentiated on the basis of the thinner sub-vertical, more steeply inclined elements, and the spacing of the paralaminae.

**Pseudotrupetostroma**
Khalfina & Yavorsky, 1971

TYPE SPECIES. *Stromatopora pellucida* var. *artyschtensis* Yavorsky, 1955.

**Pseudotrupetostroma ambiguum**
(Cockbain, 1984)
(Fig. 44)

*Hermatostroma ambiguum* Cockbain 1984: 26, pl. 13a-d.

MATERIAL. JCUF12754-7, all from Fanning River, JCUL788.

DESCRIPTION. Medium domical skeleton up to 7.5cm thick and 25.0cm wide, strongly latilaminate, with thicknesses of approximately 0.5-2.0cm. Growth surfaces gently undulose, forming enveloping surfaces. Astrorhizal traces common but obscure in hand specimen. Mamelons inferred by sporadic rises in growth surfaces. In vertical section coenosteles and coenostromes form an imperfect, closed, grid network in which coenosteles dominate. Coenosteles 5-7 per 2mm, 0.15-0.22mm thick, continuous, superposed through many coenostromes and slightly spool shaped in interlaminar space. Where preserved they show peripheral membranes. Coenostromes less continuous, 6-8 per 2mm, and are highly variable in thickness (0.05-0.22mm), commonly replaced by thin compact dissepiments, locally forming microlaminae. Coenostromes tripartite with a thin light or dark central line, dividing upper and lower divisions of skeletal material. Peripheral membranes extend onto coenostromal surfaces. Skeletal elements compact, including peripheral membranes and dissepiments. Galleries rounded

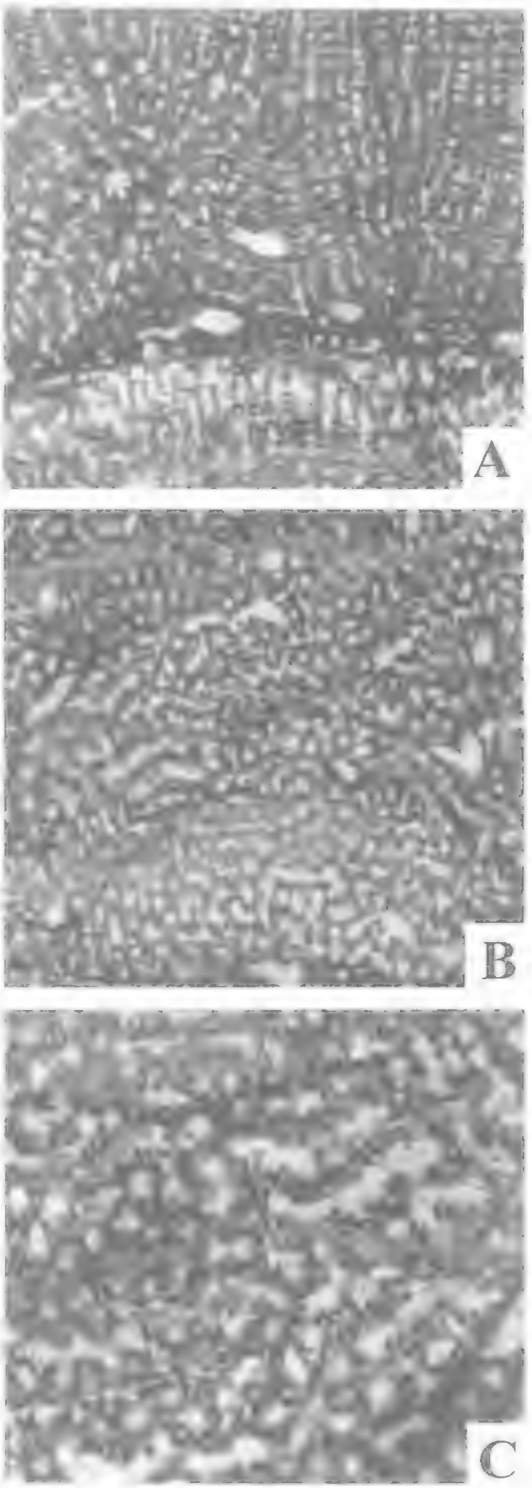



FIG. 41. *Stromatopora* sp. JCUF12028. A, vertical section × 10; B, tangential section × 10; C, tangential section × 20.

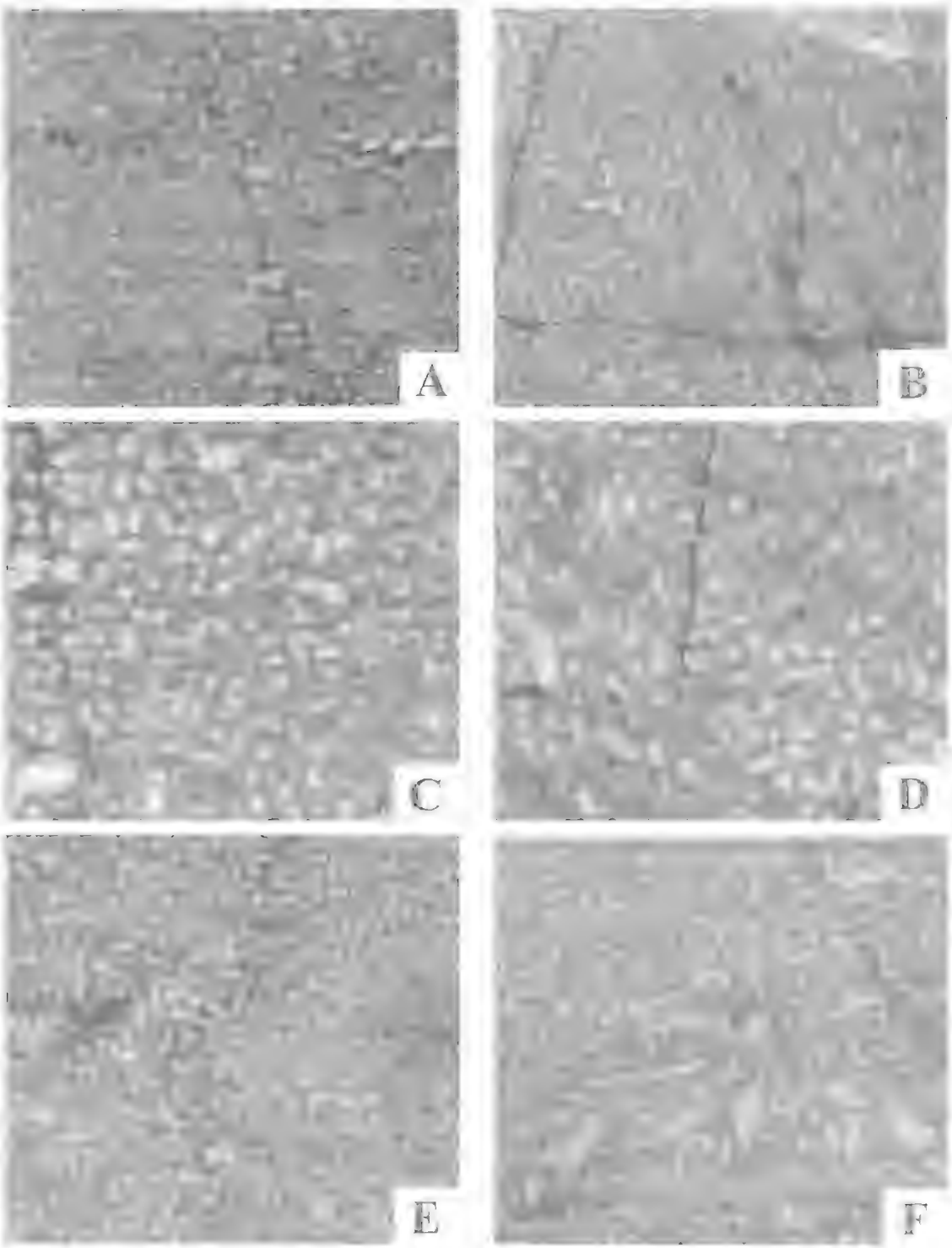



FIG. 42. *Ferestromatopora heideckeri* sp. nov. A-D, holotype JCUF11983. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D, tangential section × 20. E,F, paratype JCUF11989. E, vertical section × 10; F, tangential section × 10.

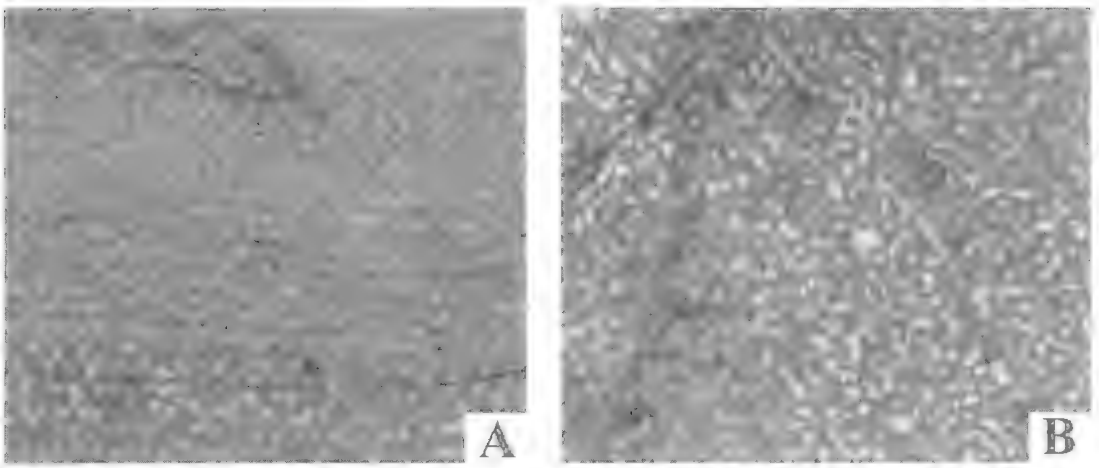



FIG. 43. *Ferestromatopora heideckeri* sp. nov. paratype JCUF11986. A, vertical section × 10; B, tangential section × 10.

in vertical section, some vertically elongate, commonly crossed by dissepiments. Astrorhizal canals wide, containing many strongly arcuate dissepiments. In tangential section skeletal elements form a closed labyrinthine network. Galleries rounded to vermiform and show, where preserved, abundant peripheral membranes. Gallery dissepiments uncommonly seen in tangential section. Astrorhizal canals walled, commonly crossed by disspeiments and form simply branched systems.

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Middle Devonian, Givetian; Canning Basin, Western Australia, Late Devonian, Frasnian.

REMARKS. The peripheral membranes, the grid-like skeletal structure, and the tripartite laminae immediately suggest this material as *Hermatostroma*. Examination of paratype material of *H. ambiguum* Cockbain, from the Canning Basin, in particular GSWA10430, has shown it to be indistinguishable from the Burdekin material. The dominance of coenosteles and the reduction of coenostromes to dissepiments in places indicates the species is better placed within *Pseudotrupetostroma*, althought the tripartite coenostromes, peripheral membranes and spool shaped coenosteles in inter-coenostromal space are problematic.

### **Salairella** Khalfina, 1960

*Salairella* Khalfina 1960: 330; Lessovaya 1970: 88; Yang & Dong 1979: 58; Stearn 1980: 892; Stearn 1983: 555; Mistiaen 1985: 145; Bogoyavlenskaya & Khromych 1985: 87; Stearn 1993: 219.

TYPE SPECIES. *Salairella multicea* Khalfina, 1961:331, pl. D-5 fig 3. from the Eifelian of Salair, Russian Federation, by original designation.

DISTRIBUTION AND AGE. Victoria, Australia, Lochkovian-Pragian; Ellesmere Island, Arctic Canada, Early Devonian, Emsian; Middle Devonian: Buchel District, Germany, Middle Devonian; England, Middle Devonian; Salair, Russia, Middle Devonian; Omulveski Mountains, Siberia Middle Devonian; Givetian: Afghanistan, Givetian; Dinant Basin, Belgium, Givetian, Guangxi, China, Givetian; Burdekin Subprovince, north Queensland, Australia, Givetian.

REMARKS. According to Stearn (1983, 1993), *Salairella* is distinguished from *Stromatopora* on the basis of the regular long coenosteles and the characteristic round, enclosed coenotubes in tangential section. The microstructure is akin to *Stromatopora*, quite unlike the unique microstructure of *Parallelopora* (Stearn, 1980, 1983, 1993).

*Salairella* has been variously placed in the Syringostromellidae by Stearn (1980, 1983) and Dong (1988), in the Stromatoporidae by Khalfina (1960), and in the Yavorskiinidae by Khalfina and Yavorsky (1969), and Dong & Song (1992). The persistence of coenosteles and preponderance of long coenotubes relates well to the Syringostromellidae.

### **Salairella buecheliensis** (Bargatzky,1881a) (Fig. 45)

*Caunopora bücheliensis* Bargatzky 1881a: 62; Flügel & Flügel-Kahler 1968: 53. (with complete synonymy pre 1968).

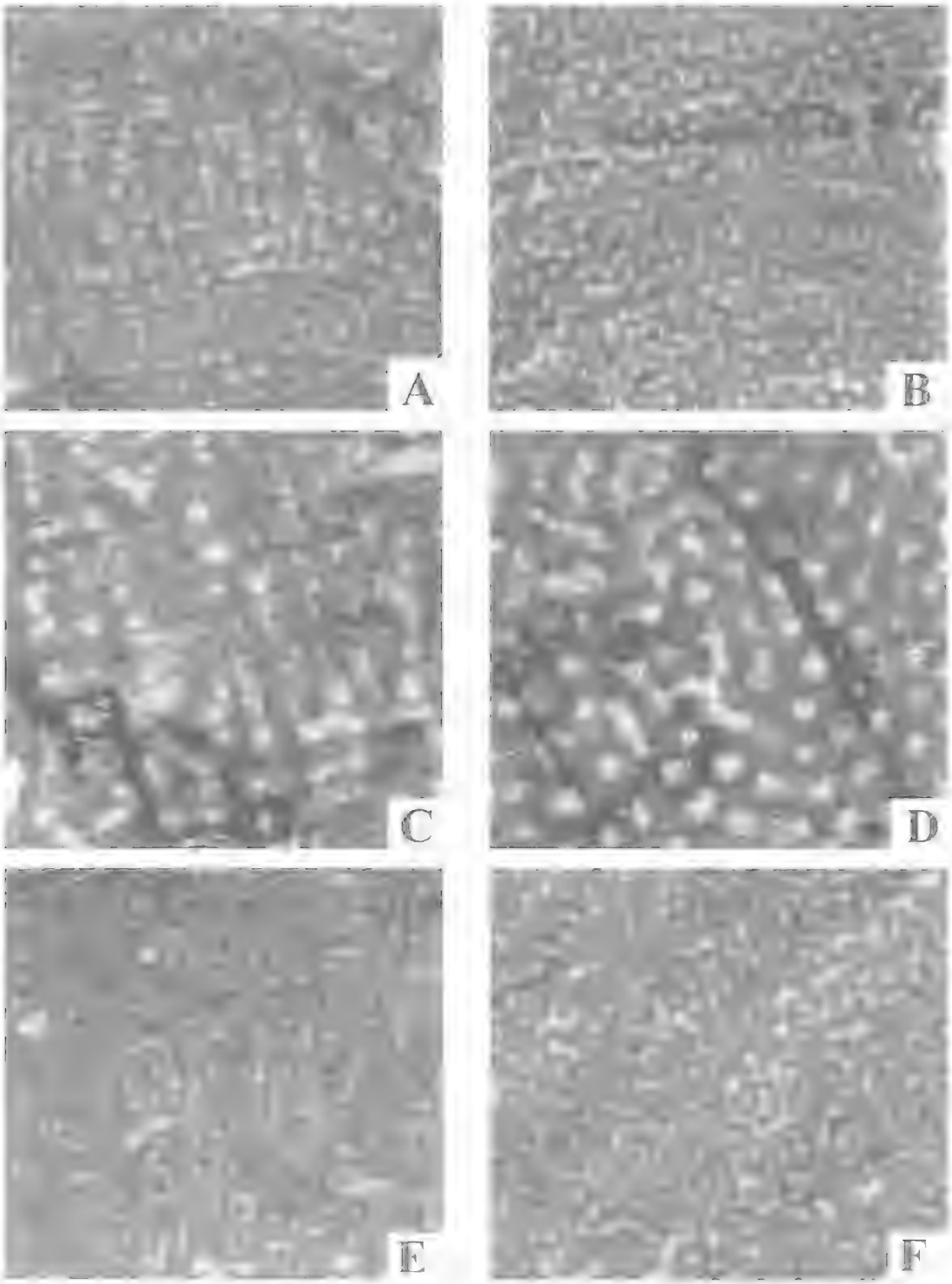



FIG. 44. *Pseudotrupetostroma ambiguum* (Cockbain, 1984). A-D, JCUF12754. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D, tangential section × 20. E, F, JCUF12756. E, vertical section × 10; F, tangential section × 10.

*Stromatopora bücheliensis* (Bargatzky), Nicholson 1886b p. 23, pl. 10, figs. 5-7.
Not *Stromatopora bücheliensis* (Bargatzky), Ripper 1937b; 187, pl. 8, figs. 9-10; Ripper 1937c; 5; Ripper 1938 p. 236.
*Parallelopora bücheliensis* (Bargatzky), Lecompte 1952: 290.
*Salairella buecheliensis* (Bargatzky), Mistiaen 1985 p. 145, pl. 12, figs. 10-12, pl. 13, fig. 1.

MATERIAL. JCUF11774, 11776, 11778, 11781, 11792, 11794, 11795, 11796 and 11804 from JCUL788; JCUF11875 from JCUL787; JCUF11903 from JCUL782.

DESCRIPTION. Skeletal shape low domical, small bulbous or irregular. Long coenosteles, 9-14 in 5mm (mean = 10.2,) relatively thick (0.2-0.3mm, mean = 0.23mm), dominate the skeletal structure. Shorter and thinner coenostroms, 0.08 -018 mm thick, often replaced by dissepiments which locally form microlaminae a few coenosteles wide. The galleries approach coenotubes (pseudozooidal tubes) in proportion. In tangential section galleries much reduced, and rounded to vermiform in cross section. Microstructure is melanospheric.

REMARKS. Placement of this species within the genus *Salairella* Khalfina is justified on the basis of microstructure, the long coenosteles and the rounded, reduced galleries in tangential section (Mistiaen 1985). The reduction of the galleries is substantially less in *S. buecheliensis* than in the type species *Salairella multicea* Khalfina. Mistiaen (1985) assigned *Caunopora bücheliensis* Bargatzky (=*Parallelopora bücheliensis* (Bargatzky) of Lecompte, 1952) to *Salairella* Khalfina, on the basis of the microstructure, the dominance of long coenosteles and the diminution of the galleries in tangential section.

**Salairella** cf. **S. cooperi** (Lecompte, 1952)
(Fig. 46)

MATERIAL. JCUF12029-34, ?JCUF12035, ?JCUF12036 from JCUL788.

DESCRIPTION. Specimens fragmental, derived from medium domical skeletons up to 13cm wide and 8cm high and not obviously latilaminate in hand specimen. In vertical section, thickened coenosteles dominate a dense skeletal network which occupies up to 70 % of the skeleton. Latilaminae, 1.5-5.0mm thick visible in thin section. Coenosteles long, commonly oblique, persisting up to 5 coenostromal thicknesses, closely spaced (10-16 per 2mm) and thick (0.15-0.22mm). Coenostromes short, oblique and subordinate to coenosteles, irregularly spaced making measurement of spacing difficult. Coenostromes thick, 0.08-0.12mm. Skeletal elements finely cellular or melanospheric. Galleries very small, rounded, commonly slightly vertically elongate. Dissepiments uncommon. In tangential section the skeletal network is dense and gallery spaces are substantially reduced; vermiform or rounded. Astrorhizae consist of simply branched walled canals, with few dissepiments.

DISTRIBUTION AND AGE. Germany, Middle Devonian; England, Middle Devonian; Dinant Basin, Belgium, Givetian; Afghanistan, Givetian; Burdekin Subprovince, north Queensland, Australia, Givetian.

REMARKS. Lecompte's (1952) illustrations of the holotype of *S. cooperi* show elongate coenosteles, and the characteristic dense skeletal framework. Burdekin material has fewer pillars per 5mm, but the overall structure of the skeleton is consistent with *S. cooperi*. Given the long vertical elements of *S. cooperi*, it is better placed in *Salairella* (see Stearn 1993).

**Salairella** sp.
(Fig. 47)

MATERIAL. JCUF12024 from JCUL788

DESCRIPTION. Laminar fragment approximately 1.2cm thick and 6.5cm in maximum width, with no obvious latilamination; upper surface silicified. Skeleton contains abundant syringoporid intergrowths, and a subordinate ?vermitid symbiont. In vertical section the structure is dominated by long, thick, persistent coenosteles, 0.15-0.40mm (mean = 0.27mm, $\sigma$= 0.06, n=10) thick, spaced 5-7 (n=5) per 2mm. Coenostromes are subordinate, thinner (0.10-0.25mm ), and generally impersistent. With vertical elements they form long coenotubal galleries, 0.13-0.30mm wide, crossed by thin, almost flat multitudinous dissepiments. Both coenosteles and coenostromes comprised of medium cellular material; dissepiments are compact. In tangential section skeletal elements dominate, galleries rounded, or less commonly short vermiform. There is a single trace of an astrorhizal canal, which is short, thin, branched dichotomously and crossed by a single dissepiment.

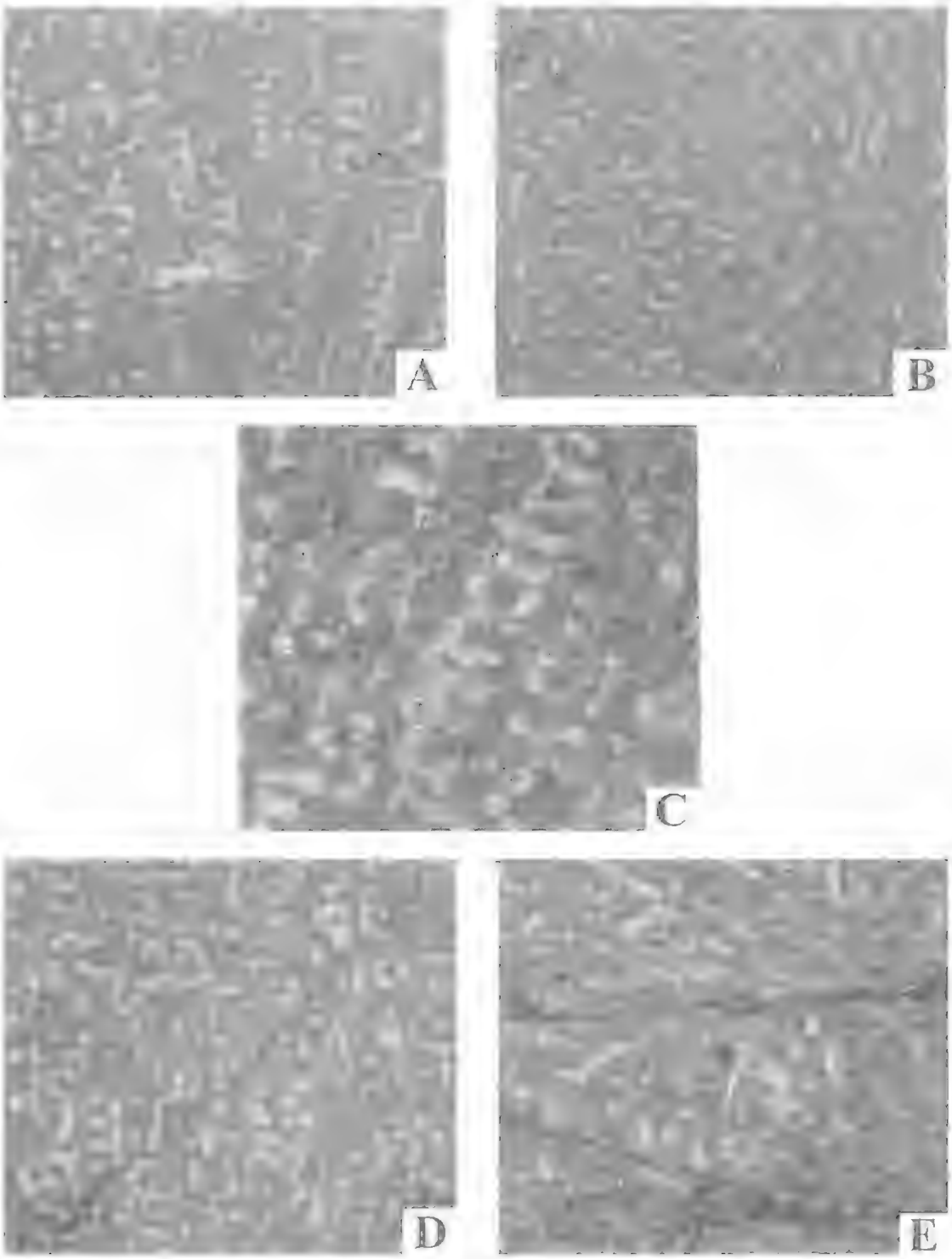



FIG. 45. *Salairella bucheliensis* (Bargatzky, 1881a). A-C, JCUF11776. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20. D,E, JCUF11774. D, vertical section × 10; E, tangential section × 10.

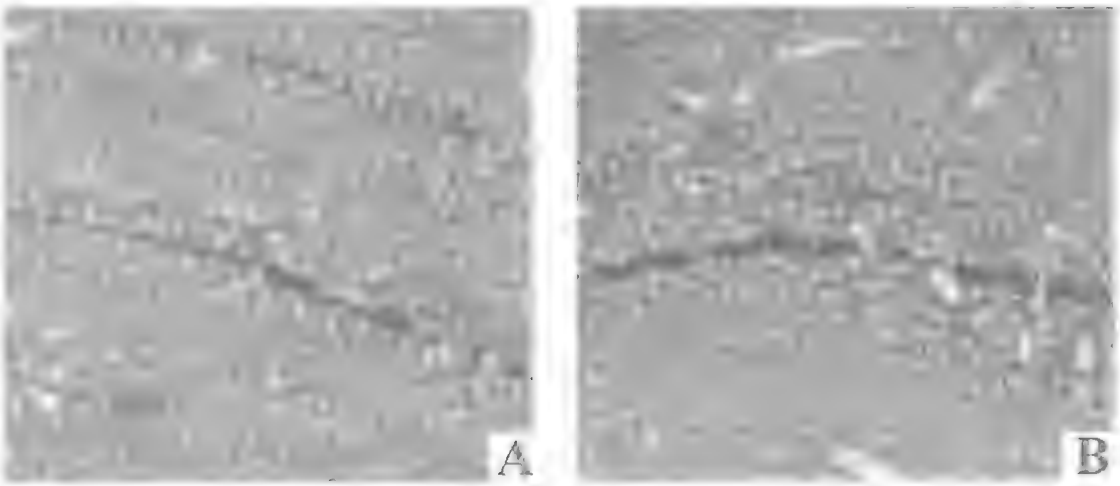



FIG. 46. *Salairella* c.f. S. *cooperi* (Lecompte, 1952) JCUF12034. A, vertical section × 10; B, tangential section × 10.

REMARKS. The occluded rounded galleries and the absolute dominance of vertical elements allies the specimen to *Salairella*. In this respect the specimen approaches the type species, *S. multicea* Khalfina (1961; fig D-5, 3a) but the elements in the Burdekin specimen are much thicker. It is separated from other Burdekin *Salairella* by the vertical element dominance, and the much thickened skeletal elements. More and better preserved material is needed before the species can be named.

**Glyptostromoides** Stearn, 1983

*Glyptostromoides* Stearn 1983: 553; Stock, St. Jean and Otte 1990; Stearn 1993: 216.
*Glyptostroma* Yang & Dong, Bogoyavlenskaya & Khromych 1985: 77; Dong 1988: 32; Stock, St. Jean & Otte 1990: 4.
In part *Glyptostroma* Yang & Dong 1979: 65, 88.
In part *Taleastroma* Galloway, Mistiaen 1985: 148.

TYPE SPECIES. *Glyptostroma simplex* Yang & Dong 1979 from the Middle Devonian (Givetian) of Guangxi, China, by original designation.

DISTRIBUTION AND AGE. Ellesmere Island, Canada, Early Devonian, Emsian;. Afghanistan, Early- Middle Devonian, Emsian to Givetian; Kuznetsk Basin, Russia Middle Devonian, Eifelian; Guangxi, China, Givetian; Burdekin Subprovince, north Queensland, Australia, Givetian.

**Glyptostromoides boiarschinovi**
(Yavorsky, 1961)
(Fig. 48A,B)

*Stromatopora boiarschinovi* Yavorsky 1961: 42, pl. 25, figs. 3-5; Khromych & Hung 1988: 24, pl. 10, fig. 2
*Glyptostroma boiarschinovi* (Yavorsky) Yang & Dong 1979: 67, pl. 36, figs. 5-6
*Glyptostromoides boiarschinovi* (Yavorsky) Stearn 1983: 553.
*Taleastroma boiarschinovi* (Yavorsky), Mistiaen 1985 p. 156, pl. 13, figs. 9-10, pl. 14, figs 1-9.
*?Neosyringostroma boiarschinovi* (Yavorsky), Kazmierczak 1971p. 118
*Syringostroma? grossum* Khromych & Hung 1988: 28, pl. 13, fig. 1.

MATERIAL. JCUF11777 and 11793 from JCUL788; 11782, 11841, and JCUF12021 from JCUL787 .

DESCRIPTION. Skeletal shape laminar to very low domical, up to 27mm high and 120mm wide. Latilaminae are in contact with neighbouring latilaminae, they may be 7-11mm apart. All specimens contain syringoporid and ?vermitid symbionts. Growth surface gently undulose without obvious mamelons. Astrorhizae indistinct. In vertical section skeleton comprised of an irregular network of short, thick, horizontal, vertical and oblique elements which is pierced by widely spaced, long, persistent, thicker coenosteles. Smaller vertical elements (coenosteles) slightly, but not obviously, dominate the irregular network. They are not persistent, only 1-2 coenostromes high. Horizontal elements (coenostroms) discontinuous, thick and subordinate. Oblique elements sporadically arise from the terminations of the short coenosteles and more commonly arise from ends of coenostroms.

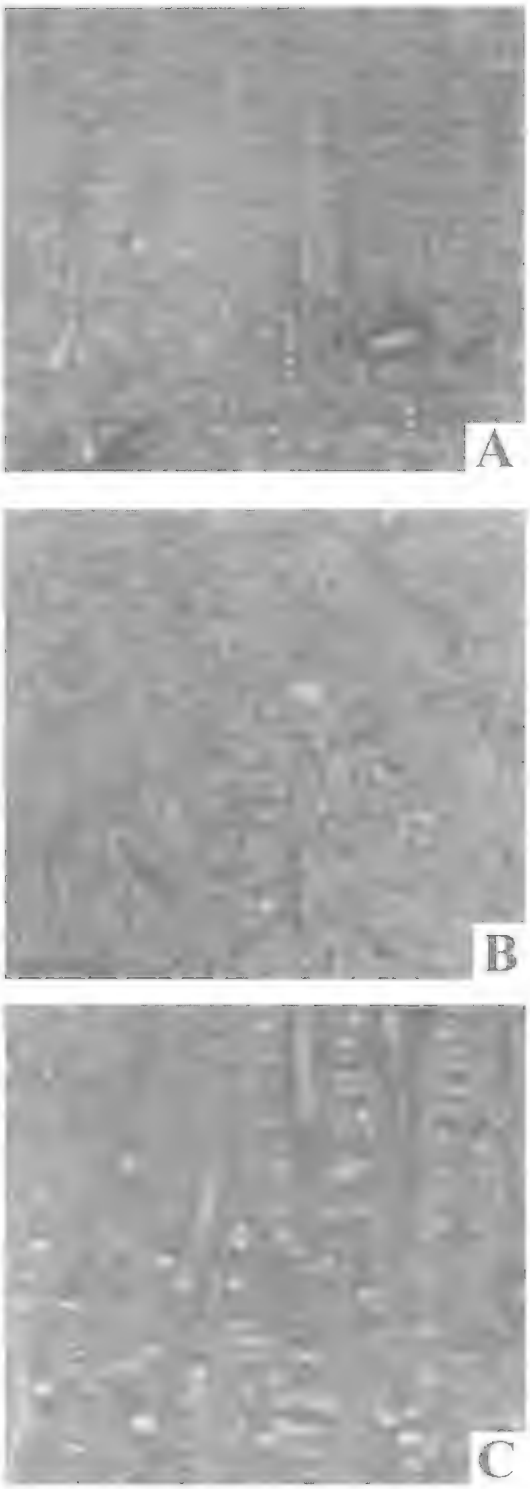



FIG. 47. *Salairella* sp. JUF12024. A, vertical section × 10. B, tangential section × 10. C, vertical section × 20.

Smaller skeletal elements equally thickened (0.15-0.22mm) consisting of diagenetically modified, now diffusely flocculent microstructure throughout the vertical section, but there are sporadic patches of conspicuously melanospheric (?altered cellular) skeletal material. Longer coenosteles penetrate up to 20 coenostroms, are somewhat thicker than smaller elements (0.22-0.30mm) and consist of sporadically melanospheric material. Long elements rarely show a persistent, dark central line. In tangential section skeletal elements form a labyrinthine network which encloses dominantly vermiform and sporadic circular galleries free of dissepiments. Melanospheric microstructure is obvious. Thicker circular pillars, and poorly connected pillars interpreted as terminations of long coenosteles, rarely show a dark centre. Commensals consists of a fine, thin, dominant syringoporid and a subordinate helically coiled ?vermitid.

DISTRIBUTION AND AGE. Salair, Russia, 'Eifelian' (=Emsian cf. Mistiaen 1985); Holy Cross Mts, Poland, Givetian. Vietnam, Middle Devonian; Guangxi, China, Givetian; Afghanistan, Givetian; Burdekin Subprovince, north Queensland, Australia, Givetian.

REMARKS. The type species *Glyptostromoides simplex* (Yang & Dong, 1979) possesses a much more enclosed network than the Burdekin material. *G. oblique* (Yang & Dong, 1979) has similar widely spaced larger coenosteles and appears to possess microlaminae (Yang & Dong, 1979, pl. 35, fig. 7). *G. luijingensis* (Yang & Dong, 1979) has much more rounded galleries in both vertical and horizontal section. The Burdekin material is conspecific with *Glyptostromoides boiarschinovi* (Yavorsky, 1961) showing a relatively open network, somewhat subdued larger coenosteles and alabyrinthine network. Mistiaen (1985) and Stearn (1993) placed this taxon within *Taleastroma*. This view is not endorsed: pillars are generally not as isolated as in other *Taleastroma* taxa listed by Stearn (1993), nor are the pillars annular (Mistiaen pl. 14, fig. 5 excepted). The larger coenosteles are submerged into the labyrinthine network, and are only rarely identifiable in tangential section. This species does show, however, a more open network than other *Glyptostromoides*. Placement in Syringostromella is precluded by the the lack of a truly open network of galleries in tangential section (Stearn, 1993).

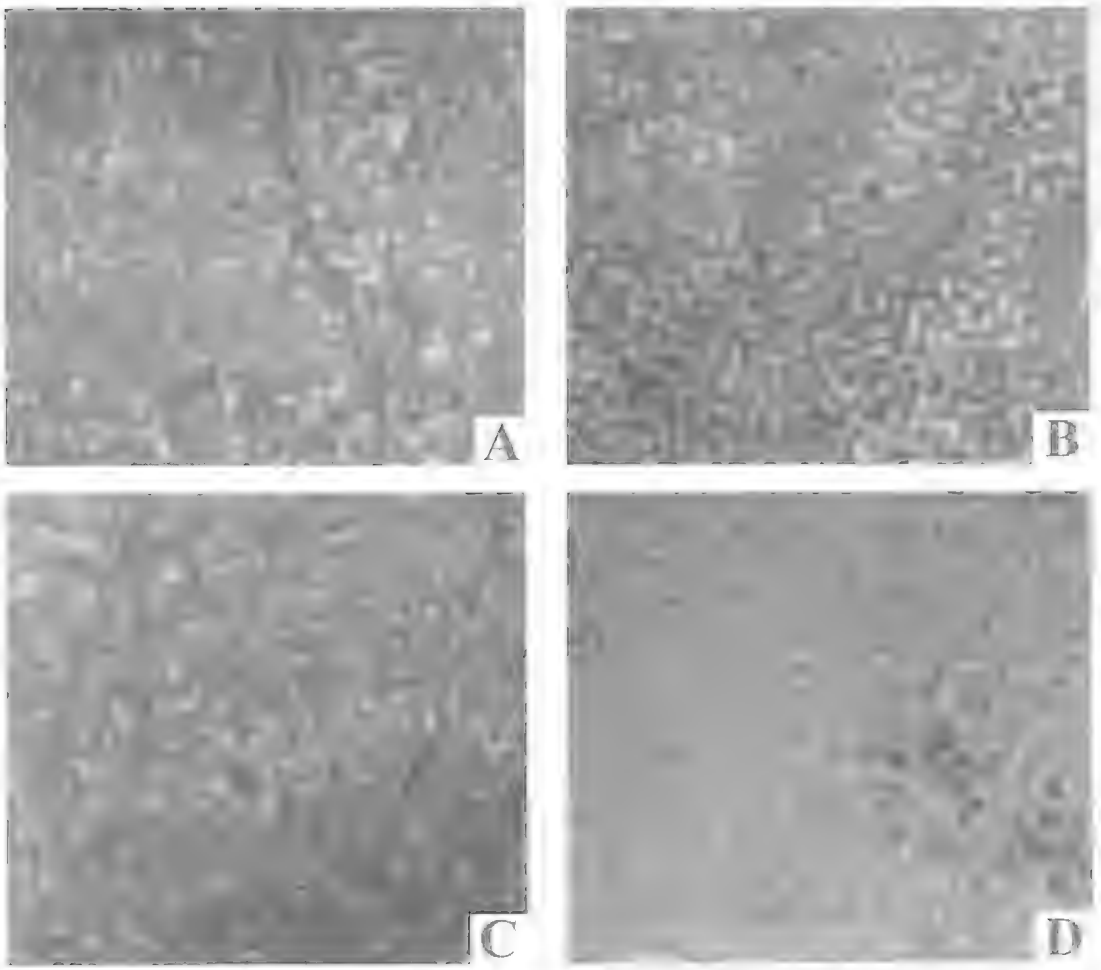



FIG. 48. A, B, *Glyptostromoides boiarschinovi* (Yavorsky, 1961), JCU I 11841. A, vertical section × 10; B, tangential section × 10. C, D, *Taleastroma* sp. JCUF12023. C, vertical section × 10; D, tangential section × 10.

**Taleastroma** Galloway, 1957

*Taleastroma* Galloway 1957: 65; Stearn 1966a: 112; Flügel & Flügel-Kahler 1968: 578; Yang & Dong 1979: 60; Stearn 1980: 892; Bogoyavlenskaya & Khromych 1985: 91; Stock, St. Jean, & Otte 1990: 8; Stearn 1993: 215.

?In part *Neosyringostroma* Kazmierczak 1971 p. 117.

In Part *Glyptostroma* Yang & Dong 1979 p. 65.

TYPE SPECIES. *Stromatopora cummingsi* Galloway & St. Jean by subsequent designation, from the Middle Devonian Logansport Limestone, Indiana.

DISTRIBUTION AND AGE. Australia, Givetian; Guangxi, Givetian, Guiezhou, China, Givetian; Afghanistan, Emsian; Indiana, United States, Middle Devonian; Belgium; Eifelian; Holy Cross Mountains, Poland, Middle Devonian.

REMARKS. Recent reviews of *Taleastroma* have been given by Mistiaen (1985) and by Stearn (1993) who has clarified the previously problematic concept of this genus. *Taleastroma* is separated from *Glyptostromoides* by the rounded pillars in tangential section, the compact axial zones of the large pillars, and the columnar pillars which are well differentiated from the cassiculate network. *T. pachytextum* of Turnsek (1970) does not represent *Taleastroma*; as it has no well developed cassiculate structure and vertical elements are overwhelmingly dominant. Stearn's (1993) assignment of *G. boiarschinovi* Yavorsky to *Taleastroma* is not accepted, as discussed previously.

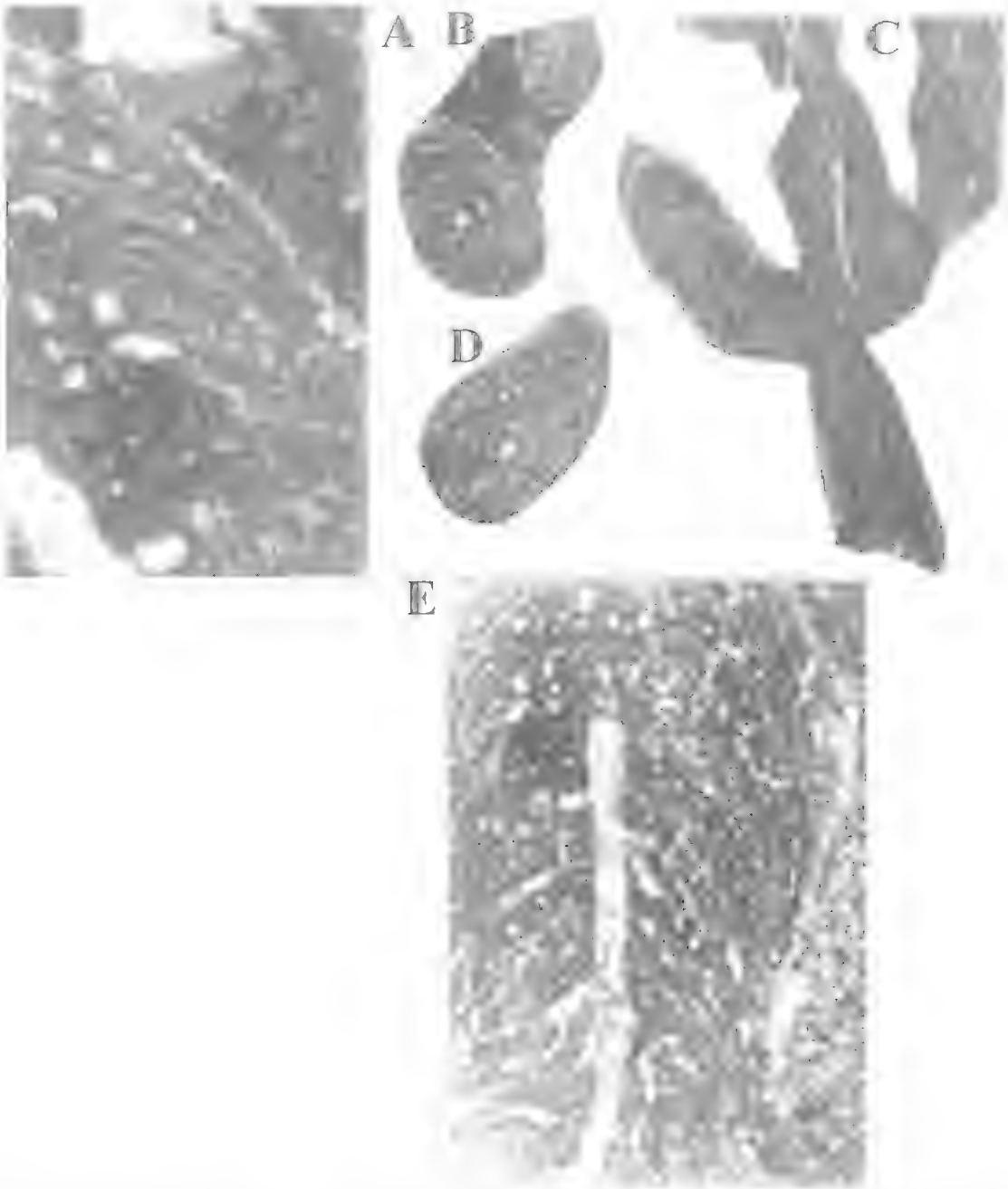



FIG. 49. A-E. *Stachyodes crassa* (Lecompte, 1952). A, JCUF11392, longitudinal section, × 25; B, JCU11393, transverse section, × 3; JCUF11392, longitudinal section, × 2; D, JCUF11291, transverse secton, × 2; E, JCUF11392, longitudinal section, × 6.

**Taleastroma** sp.
(Fig. 48C,D)

MATERIAL. JCUF12023 from JCUL788.

DESCRIPTION. Single fragment of a medium domical skeleton, with rare auloporid intergrowths. In vertical section the specimen shows only partial preservation of its original

skeleton. Moderately long, continuous pillars, 12-16 per 5mm, with conspicuous dark axes and coarsely cellular peripheries, 0.18-0.30mm thick (axis ranging from 0.08-0.15mm). Pillars dominate a disordered network of oblique to horizontal elements which are coarsely cellular, highly variable in thickness (0.08-0.25mm) and have no regular spacing. Gallery spaces irregular to rounded, with no obvious dissepiments. In tangential section the specimen is very poorly preserved. However moderately isolated pillars can be discerned.

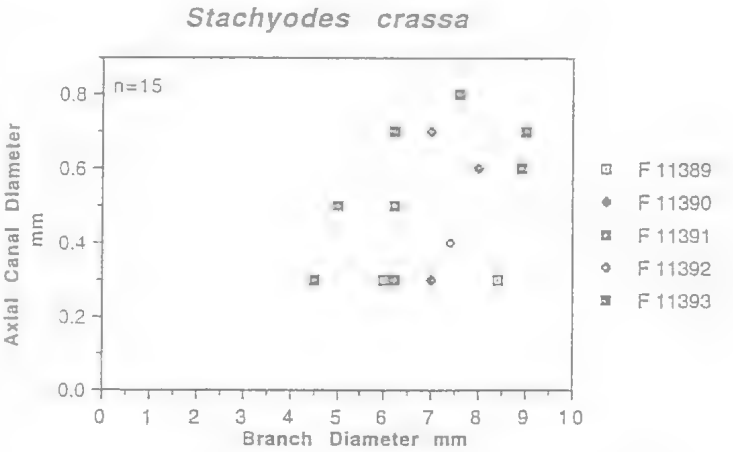



FIG. 50. Branch diameter plotted against axial canal diameter for *Stachyodes crassa* (Lecompte, 1952) from the Burdekin Formation. In this and subsequent morphometric data sets; Dx = mean branch diameter (mm), Dó = standard deviation. Ax = mean axial canal diameter (mm), As = standard deviation and n = number of branches or axial canals measured in slide.

REMARKS. The dark-centred, long pillars, dominating an essentially cassiculate network, and appearing isolated in tangential section allow confident assignment to *Taleastroma* Galloway. Lack of material and the indifferent preservation prevents specific assignment.

SYRINGOSTROMATIDA
Bogoyavlenskaya, 1969
STACHYODITIDAE Khromych, 1976

**Stachyodes** Bargatzky, 1881b

*Stachyodes* Bargatzky 1881b: 688; Nicholson 1886: 107; Pocta 1894: 138; Heinrich 1914: 38 (Translated Leverne, 1916: 58); Kuhn 1927: 547; Lecompte 1952: 298; Lecompte 1956: F136; Galloway 1957: 444; Yavorsky 1957: 58; Gogolczyk 1959: 360, 380; Galloway & Ehlers 1960: 101; Yavorsky 1961: 53; Stearn 1962: 8; Stearn 1963: 660; Yavorsky 1963: 76; Klovan 1966: 31; Stearn 1966: 116; Birkhead 1967: 85; Yavorsky 1967: 32; Flügel & Flügel-Kahler 1968: 565; Stearn & Mehrotra 1970: 17; Turnsek 1970: 24; Zukalová 1971; 96: Flügel 1974: 178; Khromych 1974: 61; Riding 1974: 572; Stearn 1975b: 1663; Khromych 1976: 68; Yang & Dong 1979: 87; Bogoyavlenskaya 1980: 8; Mistiaen 1980: 217; Stearn 1980: 892; Dong 1982a: 109; Stock 1982: 675; Dong & Wang 1984: 268; Cockbain 1984: 28; Bogoyavlenskaya & Khromych 1985: 88; Mistiaen 1985: 192; Dong 1988: 33; Mistiaen 1988: 183; Dong 1989: 174; Stock, St Jean & Otte 1990: 8; Stearn and Shah 1990: 1742.
*Sphaerostroma* Gurich 1896: 126.
*Keega* Wray 1967: 16.
(?)*Stachyodes* Fagerstrom 1982: 43.

TYPE SPECIES. *Stromatopora (Caunopora) verticillata* Mc Coy, 1851. The genus was erected by Bargatzky (1881b) based on *S. ramosa* from Paffrath, Germany but there has been considerable debate over the identity of the type species. Nicholson (1886b) regarded *S. ramosa* Bargatzky as synonymous with *Stromatopora (Caunopora) verticillata* Mc Coy, 1851.

DISTRIBUTION AND AGE. Worldwide, Eifelian to Frasnian.

**Stachyodes crassa** (Lecompte, 1952)
(Fig. 49A-E.)

*Idiostroma crassum* Lecompte 1952: 318, pl. 64, fig. 2; Flügel & Flügel-Kahler1968:. 112; Khromych & Hung 1988: 33, pl. 15, figs. 2-3.
*Stachyodes crassa* (Lecompte), Galloway & St. Jean 1957: 248; Cockbain 1984: 30, pls. 20b, 21a-c; Bogoyavlenskaya & Khromych 1985: 14.
*Stachyodes (Sphaerostroma) crassa* (Lecompte), Zukalová 1971: 104 pl. 35, fig. 1-3, pl. 37, fig. 6.

MATERIAL. JCUF11389-93 from JCUL778.

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Givetian; Vietnam, Givetian; Canning Basin, Western Australia, Givetian-Frasnian; Dinant Basin, Belgium, Frasnian; Moravian Karst, Czechoslovakia, Frasnian.

DESCRIPTION. Robustly dendroid (stachyodiform) skeletons which branch irregularly, commonly rising from a surface encrustation. Branch diameter 4.5-9.0mm (mean =6.9 , $\sigma$= 1.3, n= 15 ), bases of branches often coalesced. One, or less commonly more, axial canals. Macrostructure relatively regular,

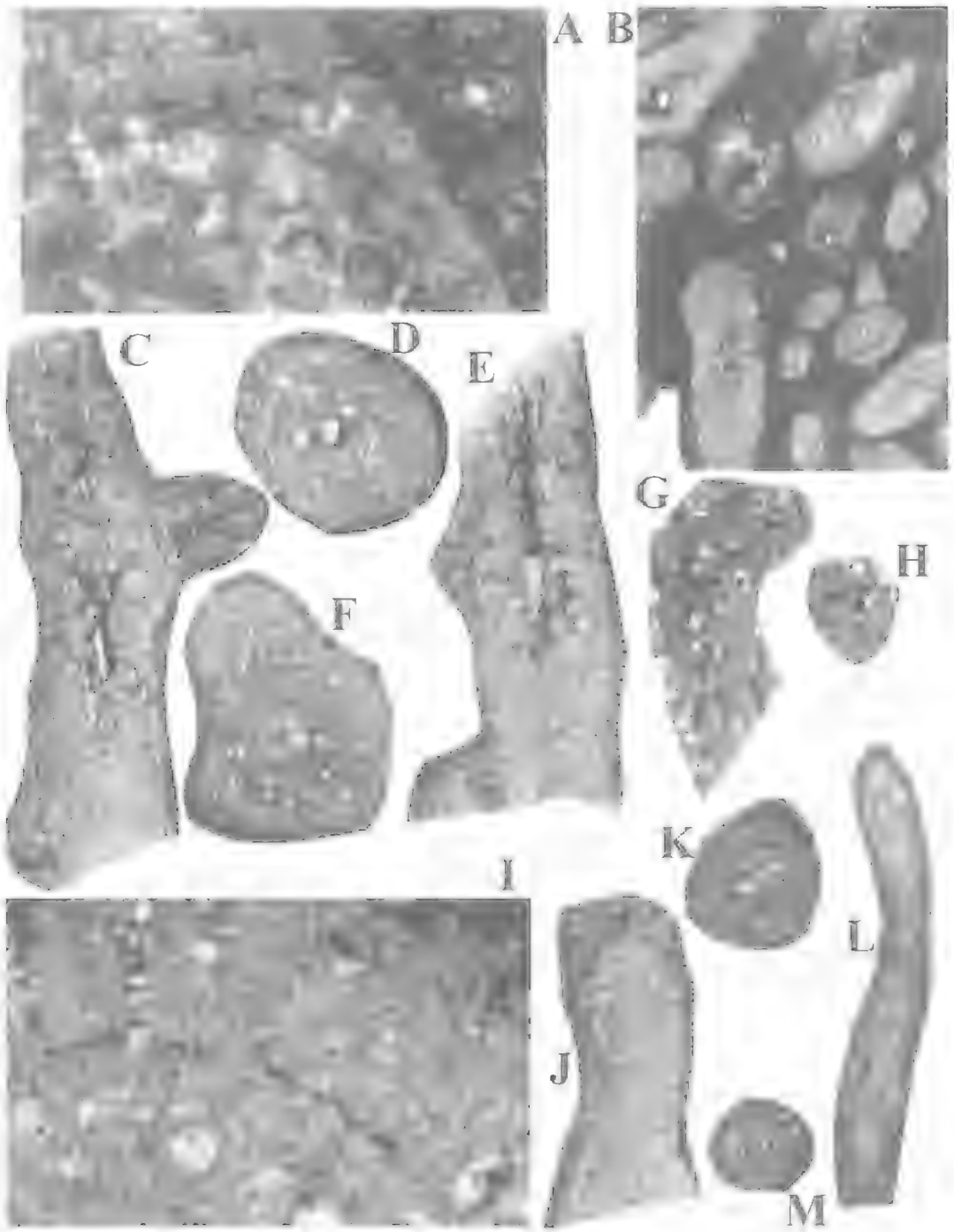



FIG. 51. A-M, *Stachyodes costulata* Lecompte, 1952. A, JCUF11395, longitudial section, ×50; B, JCUF11395, transverse section, × 2; C-F. JCUF11394; C, longitudinal section, × 3; D, transverse section, × 6; E, longitudinal section, × 3; F, transverse section, × 4; G, JCUF11401, longitudinal section, × 2; H, JCUF11401, transverse section, × 2; I, JCUF11394, transverse section, × 50; J, JCUF11394, longitudinal section, × 3; K, JCUF11394, transverse section, × 3; L, JCUF11400, longitudinal section, × 2; M, JCUF11395, transverse section, × 3.

especially at the periphery. Pillars relatively thick, 0.03-0.25mm (mean =0.16mm), and are somewhat superposed. Laminae less distinct than pillars, generally continuous, especially towards periphery, variable in thickness (0.05-0.2mm, mean = 0.12mm). Galleries oval to rounded in transverse section, elongate rounded to rectangular in longitudinal section, 0.15-0.3mm in diameter, and with rare dissepiments. Axial canals are 0.3-0.8mm in diameter (mean = 0.5, σ=0.2, n=15), regularly crossed by dissepiments. Canals intermittently branch along laminae. Microstructure near periphery tangentially (not transversely) fibrous .

MORPHOMETRICS. Morphometric data for the limited number of specimens is summarised below, and a plot of axial canal diameter against skeletal diameter is given in Figure 50.

| Specimen | D mean | Dσ | N | A mean | Aσ | n |
|---|---|---|---|---|---|---|
| JCUF11389 | 7.2 | 1.2 | 2 | 0.3 | 0.0 | 2 |
| JCUF11390 | 7.5 | 0.5 | 2 | 0.45 | 0.15 | 2 |
| JCUF11391 | 6.6 | 1.4 | 4 | 0.5 | 0.1 | 4 |
| JCUF11392 | 6.9 | 0.5 | 3 | 0.5 | 0.1 | 3 |

REMARKS. The species is distinguished by the relatively regular macrostructure in comparison to other species of *Stachyodes*. *S. costulata* is much less regular, tends to be a little smaller in branch diameter, although there is wide, overlapping variation, and has a much more dense skeletal network. Morphometric data are comparable to that given for *S. crassa* by Lecompte (1952), Zukalová (1971) and Cockbain (1984). *Stachyodes crassa* is subordinate in abundance to *S. costulata* within the Burdekin Formation.

### **Stachyodes costulata** Lecompte, 1952 (Fig. 51 )

*Stachyodes costulata* Lecompte 1952: 309, pl. 65, figs. 1-4; Gogolczyk 1959: 372, pl. 4, fig. 3, pl. 5, figs. 1-3; Stearn 1963: 660, pl. 86, figs. 4-5; Klovan 1966: 31, pl. 11, figs. 1-6; Yavorsky 1967: 34, pl. 16, figs. 1-4, pl. 16, fig. 7, pl. 18, figs. 1-3; Stearn & Mehrotra 1970: 18, pl. 4, figs.3-4. Khromych 1974: 62, pl. 16, fig. 1, pl. 17, fig. 2; Stearn 1975b: 1663; Fischbuch 1970b: 1079, pl. 148, figs. 5-7; Khromych 1976: 68, pl. 10, fig. 2; Yang & Dong 1979: 87, pl. 9,10; Dong 1982a: 287, pl. 5, figs. 3,4; Dong, 1981: 109, pl. 5, figs. 5-6; Stock, 1982: 676, pl. 4, figs. 7-9: Cockbain 1984: 28, pl. 19a-d, 20a; Bogoyavlenskaya & Khromych 1985: 14; Khromych & Hung 1988: 34, pl. 16. fig. 6; Dong 1989: 174, pl. 2, 3a-d; Stearn & Shah 1990: 1752; Webby & Zhen 1997, 51, fig 19.

*Stachyodes* cf.*costulata* Lecompte, Yavorsky 1961: 35, pl. 17, figs. 1-6; Yavorsky 1963: 124, figs. 10-12, pl. 25, figs.4-5; Yavorsky 1967: 35, pl. 17, figs. 1-6.

*Stachyodes (Stachyodes) costulata* Lecompte, Zukalová 1971, p. 101, pl. 34, figs. 5-6.

DISTRIBUTION AND AGE. Burdekin Subprovince Givetian and Broken River Province Givetian to ?Frasnian, north Queensland,; Canning Basin, Western Australia, Frasnian; Dinant Basin, Belgium, Frasnian; Holy Cross Mountains, Poland, Givetian-Frasnian; Italy, Frasnian; Czechoslovakia, Givetian-Frasnian; Timan, Russia, Frasnian; Southern Tianshan, China, Givetian; Sichuan, China, Givetian; Xizang, China, Givetian; Yunnan, China, Givetian-Frasnian; Central and Southern Guangxi, China, Frasnian; Vietnam, Givetian to Frasnian; Canada, Givetian-Frasnian; Iowa, Frasnian.

MATERIAL. JCUF11394, 11396, 11397, 11401 from JCUL788; JCUF11395 from JCUL781; JCUF11403 from JCUL778; JCUF11398 from JCUL784; JCUF11404-11409 from JCUL779.

DESCRIPTION. Robustly dendroid (stachyodiform) skeletons in some cases irregularly rising from an encrustation surface with branches 4.0-9.8 mm (mean=5.8, σ=1.3, n=27 ) in diameter. One to 5 axial canals, 0.2-0.8 mm in diameter (mean = 0.4, σ= 0.2, n= 47), regularly crossed by gently arcuate dissepiments. Skeletal material greatly thickened, producing a diminution of galleries which only become obvious at the skeletal margin where they attain diameters of 0.08- 0.18mm and are normal to the surface. Microstructure not easily discernible but is fibrous with striations parallel to the margins of the skeleton.

MORPHOMETRICS. Morphometric data are summarised below and a comparison of skeletal diameters is given in Fig. 52. $NC_m$= mean number of axial canals per branch.

| Specimen | D mean | Dσ | n | A mean | Aσ | n | NCm |
|---|---|---|---|---|---|---|---|
| JCUF11394 | 6.2 | 0.9 | 11 | 0.5 | 0.2 | 24 | 2.2 |
| JCUF11396 | 5.1 | - | 1 | 0.3 | 0.1 | 5 | 5.0 |
| JCUF11397 | 5.3 | - | 2 | 0.4 | 0.1 | 5 | 2.5 |

### NON CANALICULATE FORMS

Specimen (Dx, n); JCUF11401 (6.5, 3); JCUF11403 (9.8, 1); JCUF11399 (4.8,1).

REMARKS. *S. costulata* is more common within the Burdekin Formation than *S. crassa* and is distinguished by its dense skeletal network. The

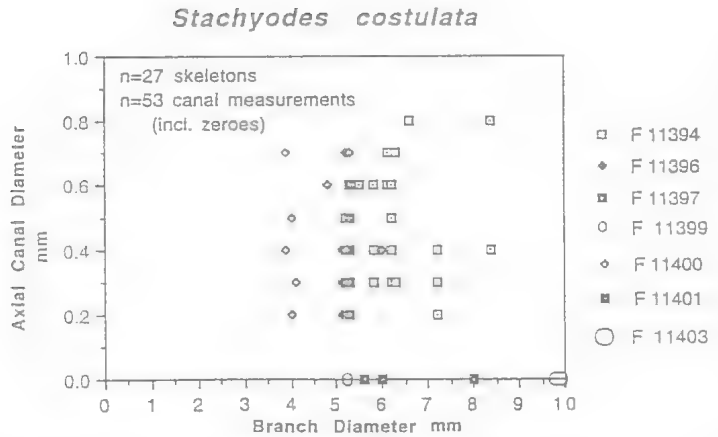



FIG. 52. Branch diameter plotted against axial canal diameter for *Stachyodes costulata* Lecompte, 1952 from the Burdekin Formation.

material compares closely with *S. costulata* of Lecompte (1952), Zukalová (1971) and Cockbain (1984). *Stachyodes costulata* Lecompte from the Stanley Limestone Member, in the Broken River Province of Webby & Zhen (1997) are indistinguishable from the Burdekin material. The species is distinguished from *S. crassa* on the basis of a much less regular network of skeletal elements. It differs in branch diameter from *Stachyodes* sp. A and *Stachyodes* sp. B. described below.

**Stachyodes** sp. A
(Fig. 53A,B.)

MATERIAL. JCUF11385-8 from JCUL788.

DESCRIPTION. Skeleton of thin branches, 1.9-3.6mm diameter (mean = 2.3, σ= 0.4, n=15), canaliculate, with axial canal 0.3-0.6mm in diameter (mean = 0.4, σ= 0.1, n=15). Microstructure unrecognisable due to poor preservation. One axial canal demonstrates a dissepiment.

MORPHOMETRICS. Data are summarised below and in Figure 54.

| Specimen | D mean | Dσ | n | A mean | Aσ | n |
|---|---|---|---|---|---|---|
| JCUF11385 | 2.4 | 0.6 | 5 | 0.4 | 0.1 | 5 |
| JCUF11386 | 2.4 | 0.3 | 4 | 0.35 | 0.05 | 4 |
| JCUF11387 | 2.4 | 0.4 | 3 | 0.5 | 0.1 | 3 |
| JCUF11388 | 2.2 | 0.2 | 3 | 0.4 | 0.05 | 3 |

REMARKS. The dendroid form and coalesced skeletal elements indicate affinities with *Stachyodes* but poor preservation renders a specific assignment impossible. The branch sizes are small for *Stachyodes*, but within the ranges of some species Cockbain (1984: 29).

**Stachyodes** sp. B.
(Fig. 53C,D.)

MATERIAL JCUF11402 from JCUL787.

DESCRIPTION. Single specimen, many slender branches 1.1-3.5mm in diameter (mean = 2.8, n=10) most commonly with axial canal 0.3-0.7mm wide (mean =0.4mm, n=9). No dissepiments observed within the axial canal. Pillars and laminae poorly differentiated giving rise to fused skeletal elements. Microstructure fibrous, normal to axial canal and skeletal margin. In transverse section microstructure has melanospheric appearance.

REMARKS. The coalesced skeletal architecture, combined with the fibrosity of the skeletal elements suggest affinities with *Stachyodes*, but the limited material precludes adequate assessment of this morph, which is best left under open nomenclature. *Stachyodes* sp. B has branches of a smaller diameter than *S. costulata* and *S. crassa*, and a more closed skeletal arrangement than the latter. It appears to differ from *Stachyodes* sp. A on the basis of its slightly larger size and the unusual microstructure

COENOSTROMATIDAE
Waagen & Wentzel, 1887

*Coenostroma* Winchell, 1867
*Coenostroma* Winchell 1867: 99; Nicholson 1886b: 11; Stock, St. Jean & Otte 1990: 3.; Stearn 1993: 221.

TYPE SPECIES. *Stromatopora monticulifera* Winchell, 1866 (p. 91) , from the Middle Devonian Traverse Group, Michigan, North America, by subsequent designation of Miller 1899.

DISTRIBUTION AND AGE. According to Stearn (1993) the genus is mostly restricted to the Middle Devonian but probably ranges from latest Silurian and throughout the Devonian. Its known geographic distribution is North America, China, Australia and Europe.

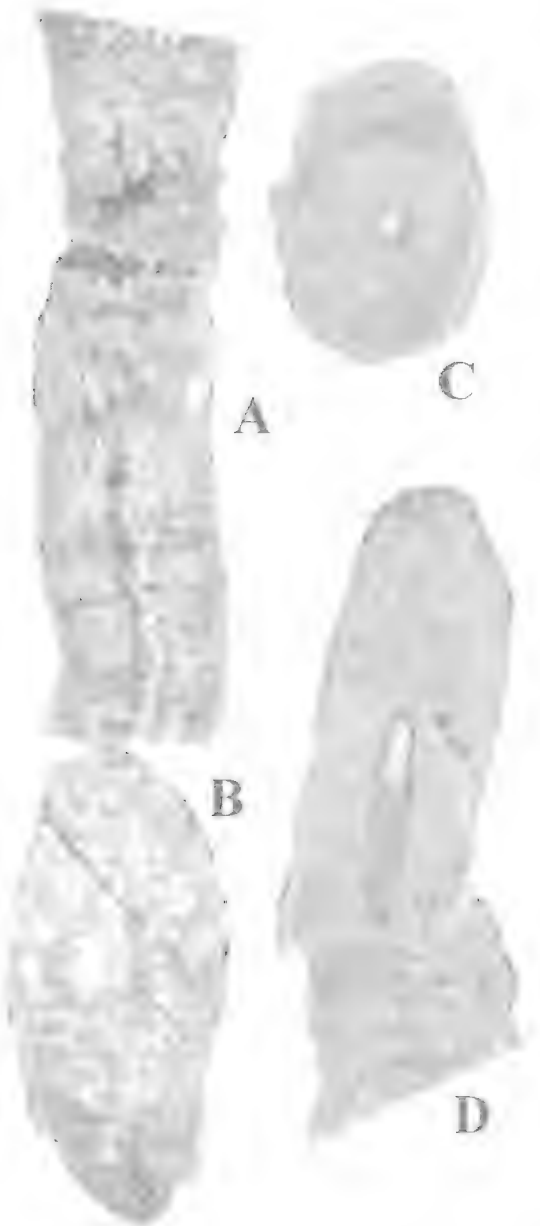



FIG. 53. A,B, *Stachyodes* sp. A. × 10 JCUF11388. A, transverse section; B, longitudinal section. C,D, Stachyodes sp. B. × 10 JCUF11402. C, transverse section; D, longitudinal section.

REMARKS. The genus has been recently resurrected and reviewed by Stearn (1993), who stressed the imperfect grid, long persistent elements and local microlaminae. He discussed the historical placement of the genus within *Stromatopora*, the reasons for its separation, and the characteristics of type material.

**Coenostroma burdekinense** sp. nov.
(Fig. 55)

ETYMOLOGY. From the Burdekin River.

MATERIAL. Holotype JCUF12763 from JCUL793; paratypes JCUF12764-6, 11788 from JCUL787; JCUF11783 from JCUL794; additional material JCUF12768-12771 from JCUL788.

DIAGNOSIS. *Coenostroma* with a relatively dense skeletal grid network in vertical section, coenosteles spaced approximately 6 per 2mm, thick and somewhat microreticulate. Coenostromes continuous and spaced approximately 5-6 per 2mm, interrupted by pores or locally replaced by microlaminae or dissepiments and composed of one or 2 microlaminae consisting of rows of melanospheres. Tangential section shows a dense, porous network, and small, rounded or irregular galleries.

DESCRIPTION. Skeletal shape low to high domical, up to 12cm wide, growth surfaces moderately to gently undulose. Common, well-spaced syringoporid symbionts are present in many specimens. In vertical section skeletal elements form a dense, moderately regular grid occupying up to 60% of the skeleton, in which coenosteles are a little more prominent than other elements. Coenosteles variable in length, some persist for up to 4 coenostromes and are generally upright, but shorter coenostromes may be oblique, commonly dividing upwards, independent of coenostroms, and consequently highly variable in thickness. Coenosteles composed of melanospheric material with the melanospheres commonly aligned, especially in thicker elements, to form a microreticulate network. Vertical elements variably spaced, 4-9 per 2mm (mean = 6.2, $\sigma$= 1.3, n=40) dependant on thickness which ranges from 0.08-035mm (mean = 0.19, $\sigma$=0.08, n=40).Horizontal elements long, commonly locally replaced by microlaminae or short dissepiments, commonly interrupted by pores. Coenostromes 4-8 per 2mm (mean = 5.2, $\sigma$=1.1, n=35), generally a little thinner than coenosteles 0.08-0.30mm (mean = 0.17, $\sigma$=0.06, n=35), commonly composed of one or 2 microlaminae or aligned, fine melanospheres completing a reticular microstructure; but may be melanospheric. Galleries small, rounded or

irregular, with common dissepiments. Uncommon astrorhizae appear as disordered groups of 1-3 subvertical septate tubes, accompanied by up-arching of coenostroms. Tangential section shows a dense skeletal network, with wide bands of dense skeleton pierced by small rounded pores dominating the skeleton. Interlaminar areas dense; galleries small and rounded to irregularly vermiform. Astrorhizae up to 8mm wide and consist of long, unwalled canals which are complexly branched at their distal ends and commonly crossed by dissepiments. Syringoporids are relatively uniformly distributed in tangential section.

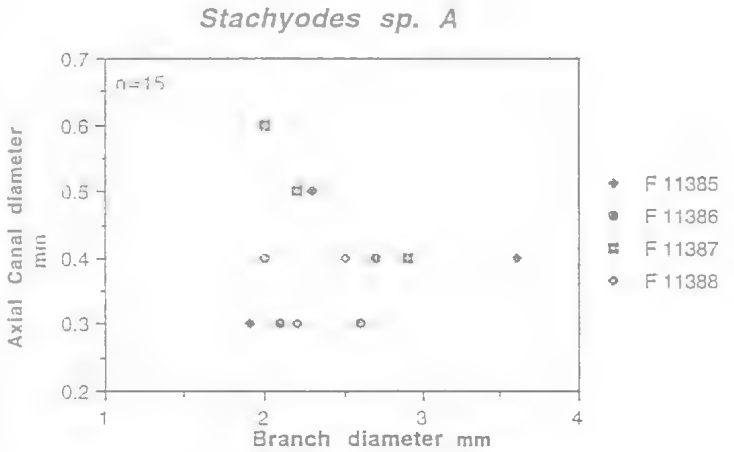



FIG. 54. Branch diameter plotted against axial canal diameter for *Stachyodes* sp. A. from the Burdekin Formation.

MORPHOMETRICS.

| Specimen | P2 | Pt | L2 | Lt |
|---|---|---|---|---|
| 12763 | 5.1 (0.7) | 0.22 (0.08) | 5.9 (1.2) | 0.16 (0.06) |
| 12765 | 7.0 (1.5) | 0.17 (0.08) | 6.0 (1.1) n=5 | 0.15 (0.06)n=5 |
| 12766 | 6.7 (1.1) | 0.19 (0.06) | 5.2 (0.6) | 0.18 (0.06) |
| 11788 | 5.8 (0.9) | 0.20 (0.06) | 5.3 (1.0) | 0.18 (0.07) |
| Average | 6.2 (1.3) | 0.19 (0.08) | 5.5 (1.1) | 0.17 (0.06) |

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Middle Devonian, Givetian.

REMARKS. The reticulate microstructure, the grid-like network and the reduced galleries place the taxon within *Coenostroma* Winchell. The type species *C. monticuliferum* (Winchell) has a similar style of skeletal organisation, but has more closely spaced skeletal elements. *C. beachvillense* (Fagerstrom) shows more isolated pillars in interlaminar spaces in tangential section. *C. burdekinense* differs from *C. wyatti* sp. nov. by having shorter coenosteles without clear axes and its somewhat more dense skeletal network in vertical section.

**Coenostroma wyatti** sp. nov.
(Fig. 56)

MATERIAL. HOLOTYPE: JCUF12040 from JCUL794. PARATYPES: JCUF12037 from JCUL794; JCUF12043-12049 from JCUL787; JCUF12050, 12051 from JCUL778; JCUF12052 from JCUL788; JCUF12053 from JCUL781.

ETYMOLOGY. For Donald Hector Wyatt, formerly of the Geological Survey of Queensland for his voluminous contributions to the geology of the Townsville hinterland.

DIAGNOSIS. *Coenostroma* which in vertical section shows a regular grid formed by long, continuous, clear-centred, peripherally melanospheric coenosteles which are spaced 9-14 per 5mm 0.07 to 0.25mm thick, spool-shaped between horizontal elements, and variable coenostroms; often long but discontinuous; spaced 8-15 per 5mm, and 0.05-0.27mm thick. Dissepiments common in the irregular to rounded galleries. Coenostromes commonly with one, or rarely, 2 microlaminae, mostly melanospheric with rare relict microreticulate structure. In tangential section elements form an irregular to labyrinthine arrangement, coenosteles vermiform to rounded where isolated with clear centres and coenostromes as arcuate zones with many rounded small pores.

DESCRIPTION. Skeleton medium to high domical, up to 8.5cm high and 9.2cm wide. Horizontal elements moderately arched forming enveloping surfaces, but only moderately undulose. Astrorhizal canals inconspicuous in hand specimen. Syringoporid symbionts abundant in many specimens. In vertical section the skeleton appears as a moderately regular grid formed by long coenosteles and long but generally discontinuous coenostroms. Vertical elements weakly dominate in some specimens, horizontal elements weakly dominate in others; in general they are equally developed.

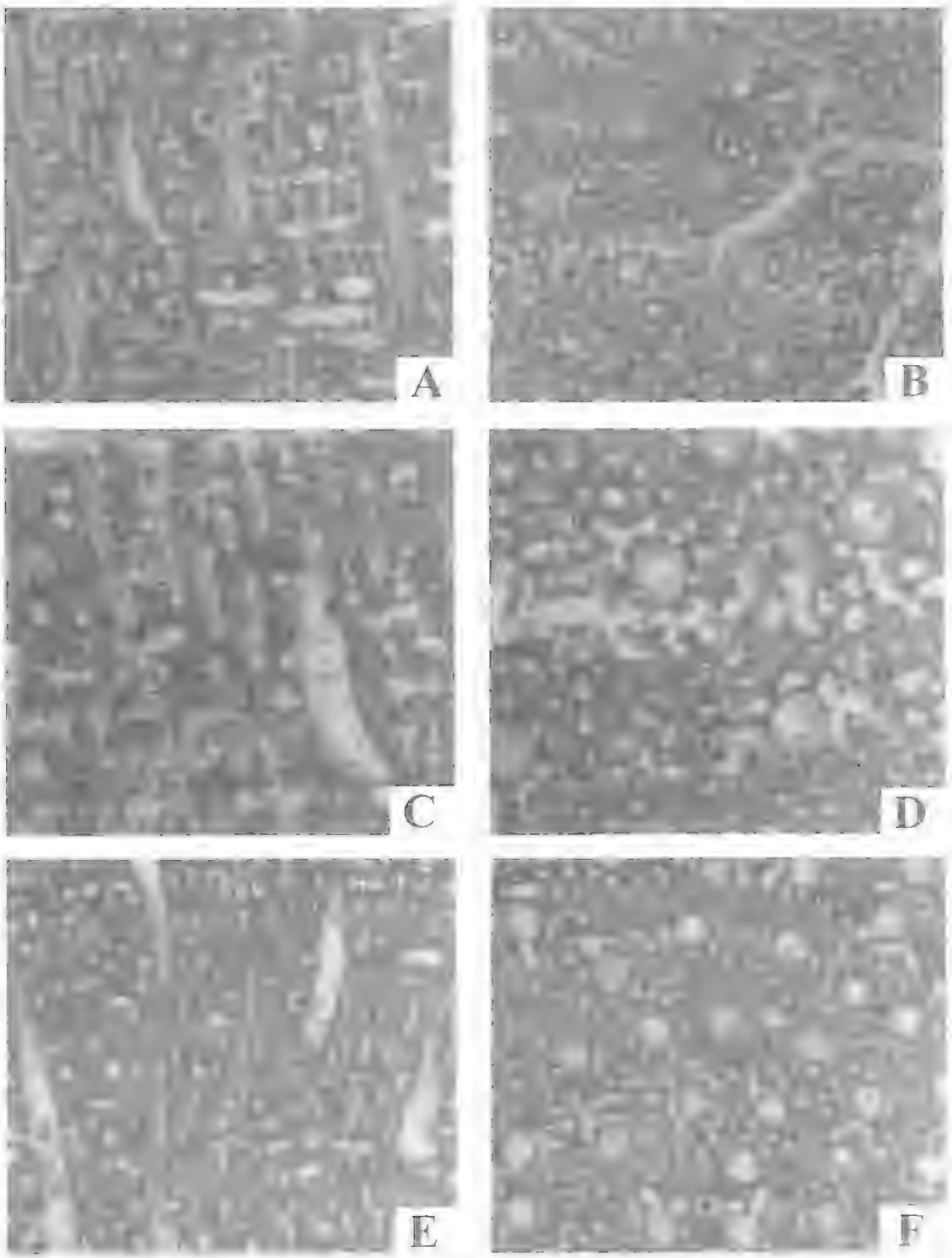



FIG. 55. *Coenostroma burdekinense sp. nov. A-D, Holotype JCUF12763. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D, tangential section × 20. E, F, paratype JCUF11783. E, vertical section × 10; F, tangential section × 10.*

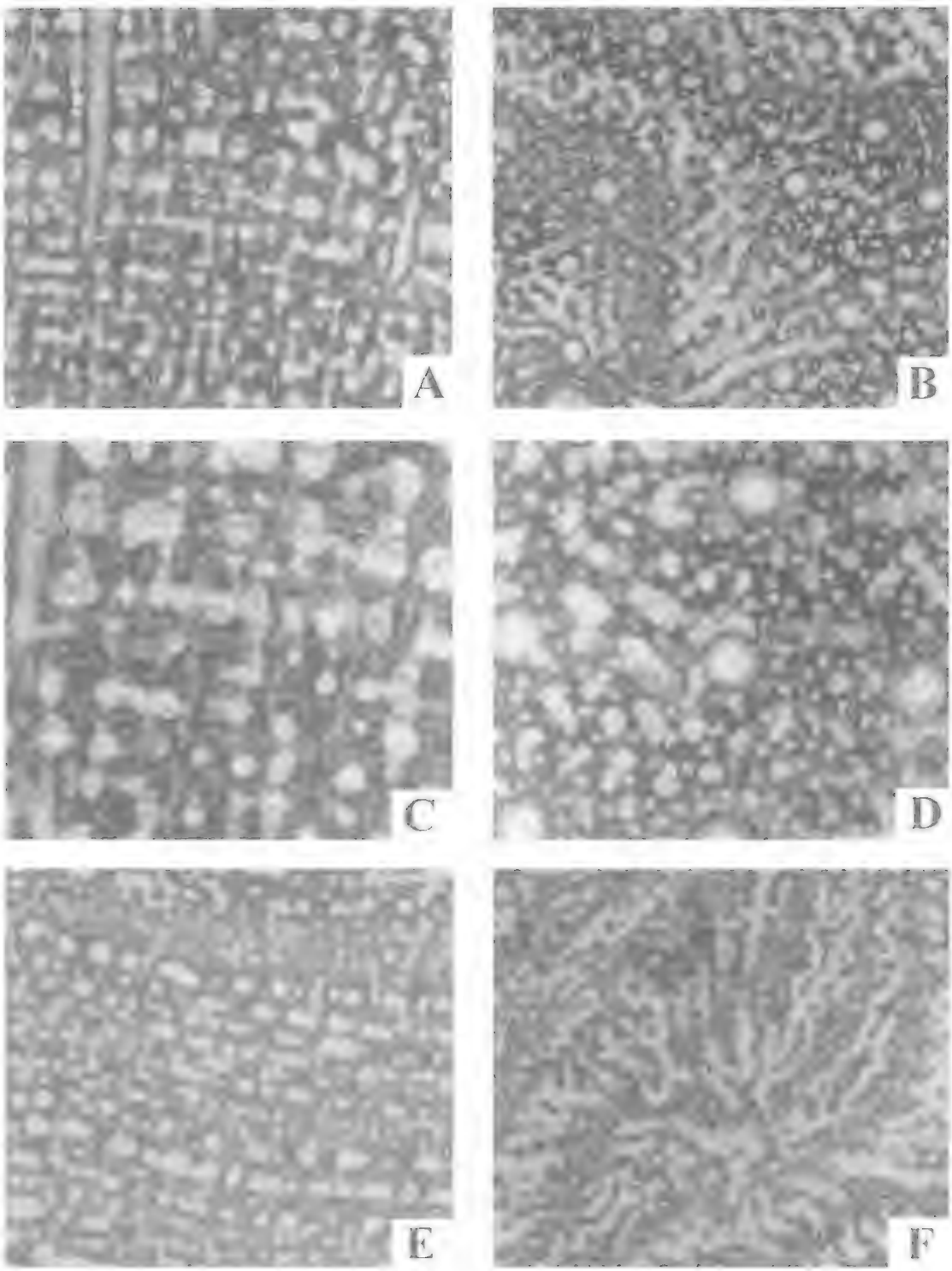



FIG. 56. *Coenostroma wyatti* sp. nov. A-D, Holotype JCUF12040. A, vertical section × 10. B, tangential section × 10; C, vertical section × 20; D, tangential section × 20. E, F, Paratype JCUF12042. E, vertical section × 10; F, tangential section × 10.

Coenosteles long, persistent for up to 16 coenostromal thicknesses, and are somewhat spool shaped in intercoenostromal space. They are 0.07-0.25mm (mean =0.16) thick, and are spaced 9-14 per 5mm (see below), with a clear axis comprising approximately half their width, with a finely melanospheric periphery. Coenostromes are of 2 types. Long discontinuous coenostromes dominate the skeletal grid, 8-15 per 5mm, 0.05-0.27mm thick. They commonly have a thin, compact, dark line, or, more rarely, 2 dark lines, which are interpreted as microlaminae. Shorter horizontal elements are irregular, sporadically oblique, with common bulbous projections on both upper and lower surfaces. They are uncommonly oblique. The coenostromes are dominantly melanospheric, but the texture varies from very fine dark spots to one or 2 larger dark spots. In places, the finer-grained melanospheres are aligned suggesting a relict, if weak, reticulate microstructure. Galleries in vertical section are rounded, or commonly irregular, vertically or horizontally elongate, sporadically forming short coenotubes. They are commonly crossed by thin, gently upwardly arcuate dissepiments. The skeletal elements are modified adjacent to syringoporid corallites; coenostromes continue unflexed to a thin (0.05-0.12mm) peripheral sheath of melanospheric skeletal material. In tangential section intersections of coenostromes form wide arcuate zones of dense skeleton. Within these zones the skeletal material is melanospheric, and abundant circular pores pierce the coenostroms. Intercoenostromal spaces are marked by pillar intersections which are short to long vermiform, less commonly rounded, with the former sporadically forming a local labyrinthine network. Pillars are commonly, especially where isolated, conspicuously clear-centred. Galleries are irregular to labyrinthine but few dissepiments are visible in tangential section. Intersections of syringoporids are surrounded by a totally enveloping sheath of skeletal material.

MORPHOMETRICS.

| Specimen | P5 | Pt | L5 | Lt |
|---|---|---|---|---|
| JCUF12038 | 11.7 (1.3) | 0.17(0.05) | 11.6 (1.0) | 0.19 (0.11) |
| JCUF12040 | 11.2 (1.2) | 0.19 (0.04) | 11.2 (1.4) | 0.19 (0.04) |
| JCUF12041 | 12.3 (1.1) | 0.15 (0.03) | 10.8 (1.4) | 0.16 (0.07) |
| JCUF12042 | 11.6 (1.1) | 0.13 (0.04) | 12.7 (1.4) | 0.15 (0.07) |
| Average | 11.7 (1.3) | 0.16 (0.04) | 11.6 (1.5) | 0.17 (0.08) |

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Middle Devonian, Givetian.

REMARKS. Assignment to *Coenostroma* is justified on the basis of the regular, if imperfect, grid in vertical section, local microlaminae and relict, but vague, microreticulate microstructure. Problems with this assignment are the fine melanospheric nature of the majority of skeletal material. The taxon is distinguished by the clear centred pillars, a feature lacking in the type species. This attribute, coupled with the melanospheric dominated-microstructure may warrant erection of a new genus. The taxon, however, can be comfortably accommodated within the generic concept of *Coenostroma* advocated by Stearn (1993) and erection of a new genus on the basis of one partially problematic taxon is not warranted.

Illustrations of the type species by Galloway & Ehlers (1960) and Stearn (1993) are broadly comparable but *C. wyatti* shows a much more regular network. *Coenostroma beachvillense* (Fagerstrom) resembles this new taxon but its horizontal elements are more prominent. *Coenostroma* sp. described by Webby, Stearn & Zhen (1993) from the Lower Devonian of Victoria also grossly resembles *C. wyatti*, but has fewer pores, no clear centred pillars, more common dissepiments and its laminae are a little more prominent.

Stearn (pers. comm.) has suggested close comparison with *Psuedotrupetostroma* Khalfina & Yavorsky, 1971. Whilst this is an attractive accomodation for this material, the relict reticultion of the microstructure is in contrast to the generic revision given by Stearn (1993). Webby (pers. comm.) and Stock (pers. comm.) have suggested the material may be accomodated within *Parallelopora*, but that genus is characterised by coarse reticulated microstructure, not the fine structure found within this taxon.

**Parallelopora** Bargatzky, 1881a.

TYPE SPECIES. *Parallelopora ostiolata* Bargatzky, 1881a, by subsequent designation from the Middle Devonian of Paffrath, Germany.

REMARKS. See Stearn (1993) for a synonymy, diagnosis and recent review.

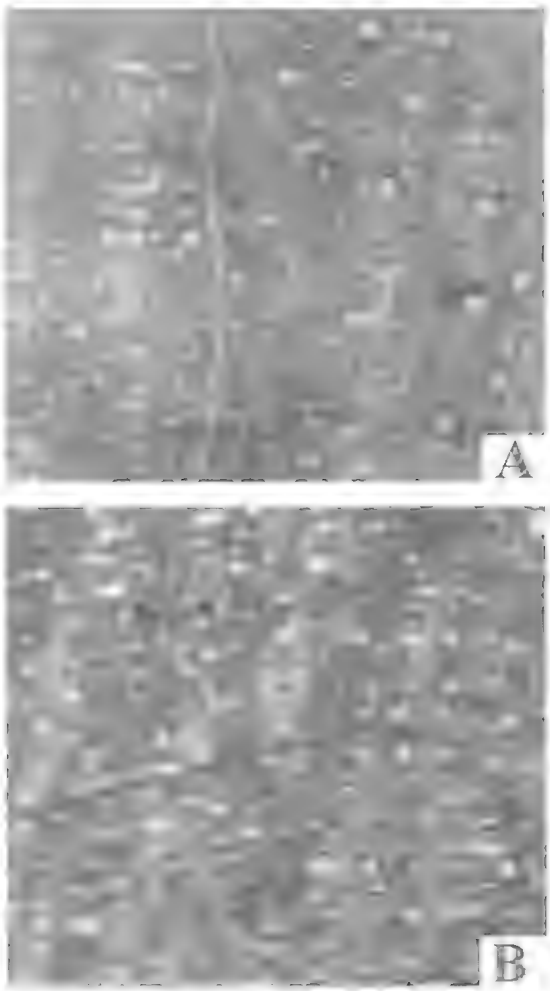



FIG. 57. *Parallelostroma* sp. JCUF12759 A, vertical section × 10. B, tangential section × 10.

?**Parallelopora** sp.
(Fig. 56)

MATERIAL. JCUF12759-62 all from Burdekin Downs, JCUL781.

DESCRIPTION. Skeleton laminar to very low domical, up to 2cm thick, fragmental so that maximum width is indeterminate. In vertical section a fine, irregular grid is formed by long, impersistent coenostromes and thick, moderately continuous coenosteles. Coenosteles are medium to long, continuous through up to 7 coenostroms, spaced at 6-9 per 2mm. They are 0.05-0.22mm thick, generally thicker than coenostroms. Coenosteles are clearly microreticulate, consisting of generally 2, but up to 4, rows of aligned melanospheres which commonly coalesce into micropillars. Coenostromes are continuous but impersistent, commonly replaced by microlaminae. They are spaced at 7-9 per 2mm, and they are generally thinner than vertical elements (0.05-0.12mm). They consist of one or 2 continuous lines of specks which very commonly form microlaminae, and combine with vertical microstructure to produce a reticulation. Galleries are very small and rounded, or vertically elongate. They are crossed by numerous dissepiments.

There are a few thin vertical or oblique tubes, interpreted as intergrowths of an indeterminate organism. In tangential section material is poorly preserved. Elements form a closed network with small rounded galleries/ coenotubes.

REMARKS. The characteristic microstructure, and the reduction of galleries in tangential section suggests affinity with *Parallelopora*, based on the revised diagnosis of Stearn (1993). The relative continuity of the horizontal elements, however, is in disagreement with this assignment and the specimen could as easily be placed within *Parallelostroma*. Coenosteles are dominant, but the horizontal elements are certainly not suppressed. The generic assignment is questionable.

ACKNOWLEDGEMENTS

This work formed the core of Ph.D. studies at James Cook University of North Queensland during 1989-1995. Professor R.M. Carter and the Department of Geology at James Cook University are thanked for provision of services during that extended period. I acknowledge the receipt of ARC Minor Grants during 1990 and URG grants in 1989 and 1991 which facilitated field work. The Queensland Museum Board is acknowledged for providing support throughout this study. I thank Prof. Bob Henderson for his supervision and consistent encouragement during the study. Profs Barry Webby, Colin Stearn and Carl Stock are thanked for their advice on previous versions of this work, and assistance in deciphering the vagaries of stromatoporoid taxonomy. Dr Yong-Yi Zhen is thanked for his advice on corals from the area. Peter Jell and Mary Wade are thanked for their encouragement. I reserve my especial gratitude for my wife Christina, for her patience, immeasurable support and assistance during the last decade.

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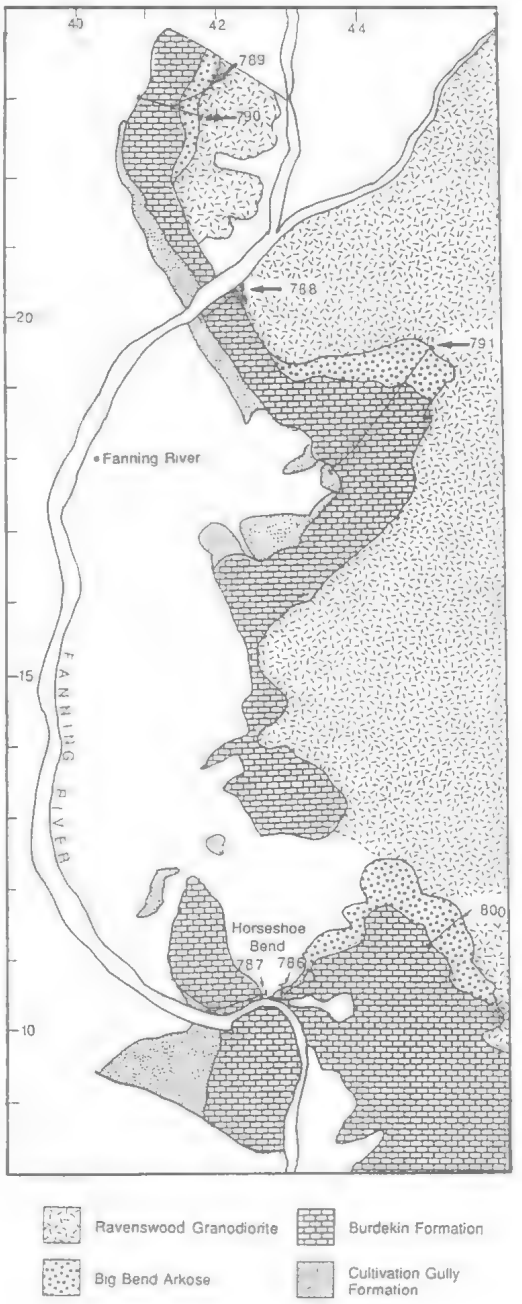



FIG. 58. (Appendix). Localities in the Fanning River area.

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# APPENDIX 1
## List of Localities (see Figs. 58,59)

| | |
|---|---|
| JCUL778 | Fletcherview station, east side of Burdekin River, downstream from 'Little Rocks'. Section from base of Fanning River Group to approximately 45m up sequence. DU155027 to DU157029. |
| JCUL779 | Fletcherview Station, north bank of Burdekin River upstream from "Little Rocks". Section from DU149025 to DU144027. |
| JCUL780 | Fletcherview Station, west bank of Burdekin River, downstream from Little Rocks. Section from lower Burdekin Formation, upwards (NE) 40m. DU153030 to DU157031. JCUL781Burdekin Downs Station, North Bank of Burdekin River downstream from confluence of Arthurs Creek. Section from lower Burdekin Formation at DU171032 to top of prominent cliffs at DU169035. |
| JCUL781 | Fletcherview Station, west bank of Burdekin River, downstream from Little Rocks. Section from lower Burdekin Formation, upwards (NE) 40m. DU153030 to DU157031. |
| JCUL782 | Western equivalent of main framestone unit in JCUL781 at DU167036, downstream from confluence of Arthurs Creek, Burdekin River, Burdekin Downs Station |
| JCUL783 | Small un-named tributary of Arthurs Creek, joining at western side of Arthurs Creek near confluence with Burdekin River at DU165040. Burdekin Downs Station Creek bank section of Big Bend Arkose. |
| JCUL784 | North bank of Burdekin River, Burdekin Downs Station, approximately 2km upstream from homestead. A short section through the Big Bend Arkose- Burdekin Formation transition at DU180024. |
| JCUL785 | Hill directly behind Burdekin Downs Station homestead, at DU200 012. (Small bivalve collection from Burdekin Formation). |
| JCUL786 | Tributary of Fanning River at Horseshoe Bend west of Horseshoe Bend Mill, Fanning River Station. Short section from unconformity to lower Burdekin Formation at DU428105 |
| JCUL787 | North Bank of Fanning River at Horseshoe Bend, section along River running east to west from DU425105 to 418103 along river flat. |
| JCUL788 | Fanning River Type Section, Fanning River, Upstream from Fanning River Station from DU422204 to DU417202 |
| JCUL789 | Fanning River North Section, approximately 3km N of Fanning River type section, in gullies from DU419232 through forest clearing at DU413230 to DU410230. Big Bend Arkose to uppermost Burdekin Formation. |
| JCUL790 | Section in gully approximately 3km N of Fanning River Type section, through Big Bend Arkose and lowermost Burdekin Fmn. From DU417228 to DU414229. |
| JCUL791 | Section across main limestone hills SE of Fanning River type section, comprising all of the Burdekin Formation at its thickest mapped point. DU448194 to DU433178. |
| JCUL792 | Big Bend, Burdekin River, Burdekin Formation only from DU093055 to DU091052. |
| JCUL793 | Outcrop in un-named creek from base of Fanning River Group at DU185 026 upstream for approx 100 metres. Burdekin Downs Station. |
| JCUL794 | Isolated rubblecrop containing abundant well preserved stromatoporoids, N of JCUL781 at DU176037 Burdekin Downs Station. |
| JCUL795 | Rubblecrop along fenceline, on hill 2km N of Burdekin Downs Homestead at DU205 029. |
| JCUL796 | Kirkland Downs, immediately S of road into property at 993604 (Hillgrove 1:100 000). |
| JCUL797 | Turkey Hill, Kirkland Downs Station, 2km to the West of station residence at 979621 (Ewan). |
| JCUL798 | Paynes Lagoon Station, 200m south of Boundary Creek, approximately 800m to the west of cattle yards at 045 467 (Rollingstone). |
| JCUL799 | Paynes Lagoon Station, 400m E of Boundary Mill in Boundary Creek 062 470 (Rollingstone). |
| JCUL800 | In Hills 1km NNW of Golden Valley. Section through Big Bend arkose from DU451115 to 448113. |
| JCUL801 | Mount Podge, Laroona Station, Section from northern edge of rhyolite intrusion to top of Mount Podge Limestone along Running Creek. Laroona Formation and Mount Podge Limestone from 915 639 to 913 649 (Ewan). |
| JCUL802 | Mount Podge Eastern section. Approximately 600m E of Running Creek Section from basal sandstones East of un-named gully N to same Gully, offset 200m E in gully and thence N to base of Keelbottom Group at foot of hill from 920 639 to 920 641 and 922 641 to 921 647 (Ewan). |
| JCUL803 | Fanning River Caves, Rope Ladder Cave, 18m section of Burdekin Formation, through 3 main chambers. 3km SE of Fanning River Station.; part of JCUL791 section DU452 182. |
| JCUL804 | Short section, SW side of Burdekin River at Fletcherview Station, almost opposite JCUL782 with resepect to river DU163 035. |
| JCUL805 | Arthurs Creek, small section thorugh basal units at DU169048. |
| JCUL806 | Mount Podge West section through Limestone approx 2km west of Running Creek, south of main peak at Mount Podge from 892 644 to 895 648 (Ewan). |

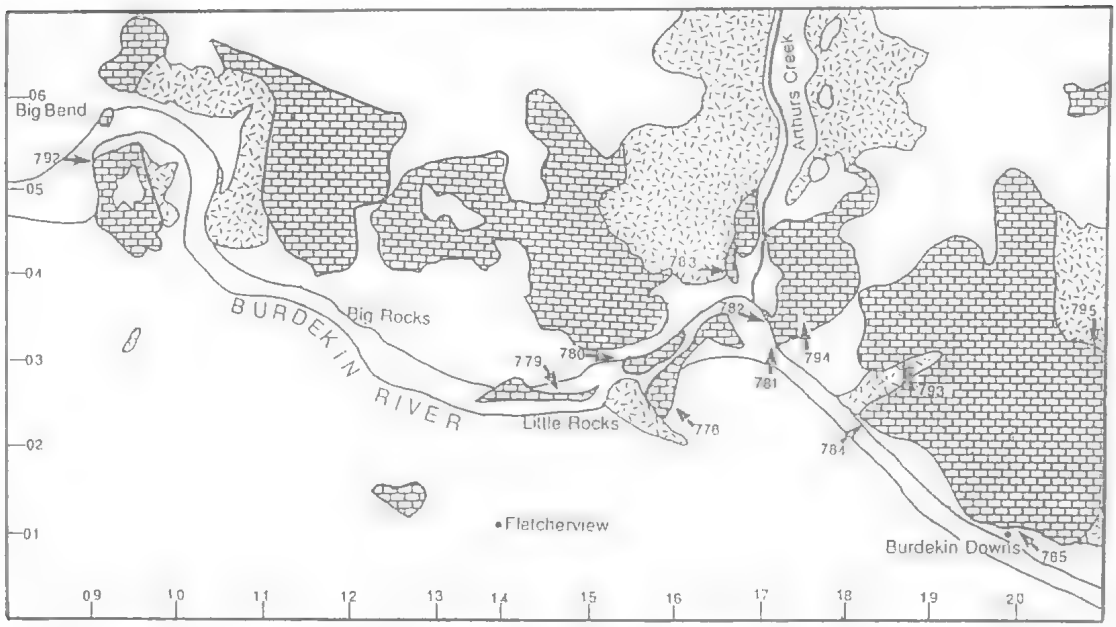



FIG. 59. (Appendix). Localities in the Burdekin Downs-Fletcherview area.

***WESTRALIADISCUS* GEN. NOV. A REPLACEMENT NAME FOR *NINGBINGIA* COOK.** *Memoirs of the Queensland Museum 43(2): 552. 1999* :- *Ningbingia* , with type species *N. robertsi* Cook 1998 was erected for a large tropidodiscine from the Westwood Member of the Hargreaves Formation, Late Devonian (Frasnian), Bonaparte Gulf Basin, Western Australia. The name is invalid as it is preoccupied by the modern pulmonate *Ningbingia* Solem 1981. I propose the new generic name *Westraliadiscus* gen. nov. in replacement of *Ningbingia* Cook, 1998. The name is for the state of Western Australia.

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# AUSTRALIAN SPECIES OF SOLENOCERIDAE (PENAEOIDEA: DECAPODA)

W. DALL

Dall, W. 1999 06 30: Australian species of Solenoceridae (Penaeoidea: Decapoda). *Memoirs of the Queensland Museum* **43**(2): 553-587. Brisbane. ISSN 0079-8835.

Twenty-seven species of Solenoceridae from Australian seas, including one new species, have been identified (* indicates new records): **Cryptopenaeus clevai*, *C. crosnieri*, *Gordonella kensleyi*, *G. paravillosa*, *Hadropenaeus lucasi*, *Haliporoides cristatus*, *H. sibogae*, **Haliporus taprobanensis*, **Hymenopenaeus aequalis*, *H. halli*, **H. neptunus*, *H. propinquus*, *Mesopenaeus brucei*, **Solenocera alfonso*, **S. annectans*, *S. australiana*, **S. barunajaya*, **S. bifurcata* sp.nov., *S. choprai*, **S. comata*, *S. faxoni*, **S. koelbeli*, **S. melantho*, **S. moosai*, **S. pectinata*, **S. pectinulata*, *S. rathbuni*. Definitions of the family and Indo-West Pacific genera, with a key, are included. Keys to the Indo-West Pacific species are given, together with diagnoses of the Australian species and all diagnoses are accompanied by figures. The zoogeography of the Solenoceridae is discussed briefly. ❐ *Indo-West Pacific, Soleniceridae, Australia, diagnoses, distribution, zoogeography.*

*W. Dall, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 10 November 1998.*

Of the 5 families included in the Penaeoidea (Penaeidae, Solenoceridae, Aristeidae, Benthesicymidae, Sicyonidae) only the species of Penaeidae are well known in Australia (e.g. Dall, 1957; Racek & Dall, 1965; Grey et al., 1983). This is because they are mostly inhabitants of inshore, often shallow waters and some are of considerable commercial importance. In contrast, only 2 species of the Solenoceridae are included by Grey et al. (1983). Kensley et al. (1987) recorded another five known species plus a new species, bringing the total to eight and a further two new species have been described from Australian waters (Pérez Farfante & Kensley, 1985; Crosnier, 1986). The majority of species of the Solenoceridae occur in offshore, deeper waters and are only collected by special or exploratory trawling, but such collections over the last 25 years have shown that there is a much larger range of species than was thought previously . Twenty-six species out of a total of 45 authentic Indo-West Pacific species are now recorded from Australian seas.

There have been a number of key taxonomic papers on solenocerids in recent years by Crosnier (1978, 1984, 1985, 1986, 1988, 1989, 1994a,b) and by Pérez Farfante (1977, 1981 and co-authored papers). Unfortunately, the literature is rather scattered, often in publications not readily available to Australian biologists, is in four languages besides English and mostly on specimens from outside Australian waters. This paper therefore attempts to cover the Australian species in sufficient detail to facilitate identification of local species by fisheries biologists and other non-specialists. As well as 25 known species it includes 1 new species. Definitions are given of the family and eight genera, with keys. Keys to the species of each genus include known Indo-West Pacific species, because it is likely that, in the future, some additional species will be found in Australian seas. The species diagnoses and figures are from specimens in the collections of the Queensland Museum (QM), the Museum & Art Gallery of the Northern Territory (NT) and the Western Australian Museum. All figures were drawn using a stereomicroscope with a camera lucida.

## DEFINITIONS

*Special taxonomic features.* Traditionally, the characteristics of the genitalia (petasma and/or thelycum) have been used as the primary features for specific identification of Penaeoidea, particularly in genera with similar external morphology. The disadvantage of such a system is that, in penaeoids, often specimens of only one sex are available, or the specimen is a juvenile. In the Solenoceridae, however, the majority have sufficient distinctive features of the cephalothorax and abdomen, particularly the former, to enable a positive identification to be made. The genitalia have therefore often not been included in species diagnoses and figures in this paper, unless the features of the genitalia are essential for identification. A complete identification

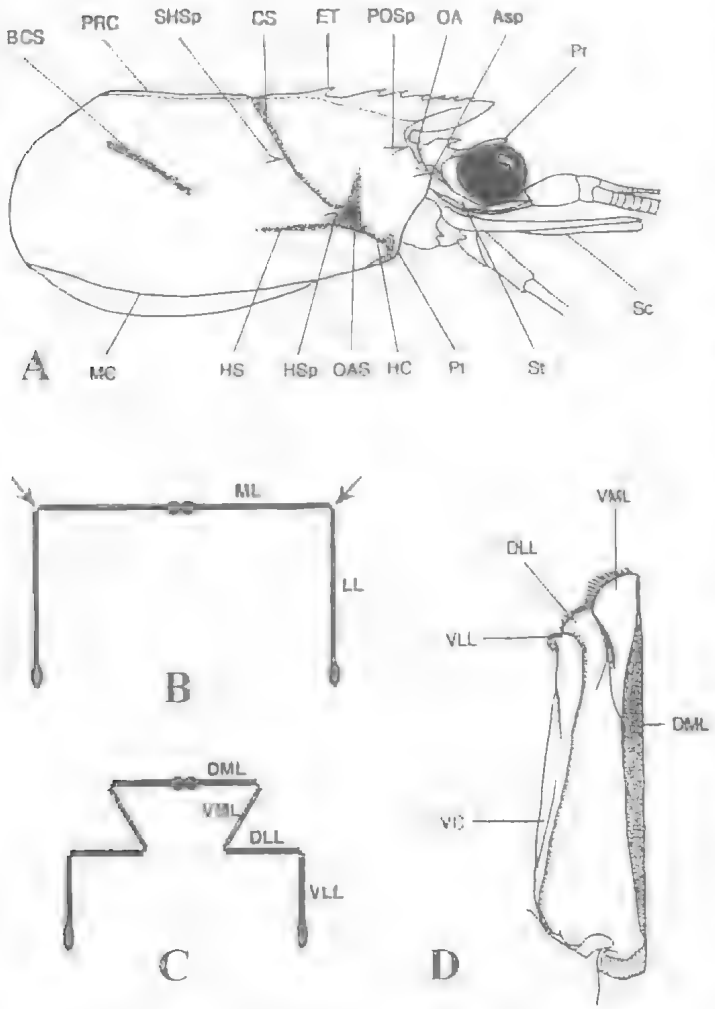



FIG. 1. A, features of taxonomic importance on the cephalothorax of a solenocerid. Asp, antennal spine; BCS, branchiocardiac sulcus (a carina may also be present); CS, cervical sulcus and carina; ET, epigastric tooth (the next tooth is the first rostral tooth); HC, hepatic carina; HS, hepatic sulcus; HSp, hepatic spine; MC, marginal (or sub-marginal) carina; OA, orbital spine (may be only an angle); OAS, orbito-antennal sulcus; POSp, postorbital spine; PRC, postrostral carina; Pr, prosartema; Pt, pterygostomial angle (may be a spine); Sc, scaphocerite; SHSp, suprahepatic (or postcervical) spine; St, stylocerite. B, diagrammatic cross-section of an immature petasma before folding has taken place. The junction of the two halves by cincinnuli is indicated by two solid circles; arrows indicate the direction of infolding; ML, median lobe; LL, lateral lobe. C, cross-section after folding has taken place. DML, dorsomedian lobule; VML, ventromedian lobule; DLL, dorsolateral lobule; VLL, ventrolateral lobule. D, ventral aspect of the right half of a solenocerid petasma; VC, ventral costa; other letters as in B. In a petasma such as this the cincinnuli would extend for the full length of the inner edge of the dorsomedian lobule.

should, of course, include consultation with full descriptions in the literature, which usually include the genitalia.

*Cephalothorax*. The principal taxonomic features of the cephalothorax of a solenocerid are shown in Fig. 1A. By convention, only half the cephalothorax is shown. Setae have been omitted in all figures of cephalothoraxes, as these are often dense in the Solenoceridae and obscure essential features. Although 'carina' literally means 'a keel', in penaeid taxonomy it is sometimes interpreted to mean a barely discernable, flattened ridge. Such cases as these have not been included as a carina in either the diagnosis or figure. If a carina is included in the diagnosis it usually means an obvious sharp, or at least angular ridge and is shown mostly as an unbroken line. Sulci are included if they are clearly visible and are depicted as stipple.

In six of the eight solenocerid genera the orbito-antennal sulcus runs from near the rim of the orbit to the vicinity of the hepatic spine without a break (although it may be quite weak). In many *Solenocera* species, however, only the posterior part is present (Fig. 1A). It may be deep and extends almost vertically towards the base of the postorbital spine, where it ends and thus could be regarded as an antennal or postantennal sulcus. In other *Solenocera* species there is a weak orbital part indicating that it is a true orbito- antennal sulcus.

The names given by taxonomists to features of the cephalothorax are sometimes not uniform. For example, the postorbital spine may be called a postantennal spine when it is positioned behind the antennal spine, as it is in some genera; the suprahepatic spine is also called the postcervical spine. Definitions and figures of other

anatomical features not shown in Fig. 1A may be found in Dall et al. (1990).

*Petasma* (Fig. 1B-D). The petasma is developed from the inner rami of the 1st male pleopods and is used to form and implant the spermatophore in the thelycum of the female. In the Solenoceridae the petasma is basically simple, each half being comprised of two longitudinal lobes and coupled with the other half by a median dorsal row of cincinnuli. These lobes are the median and ventral lobes, united by a flexible junction, shown diagrammatically in Fig. 1B. The lobes are in turn subdivided and have been named dorsomedian, ventromedian, dorsolateral and ventrolateral lobules, respectively. They are infolded upon one another to form a channelled structure (Fig. 1C). The thickened free ventral margins are the ventral costae. The distal ends of the lobules may be simple or developed into elaborate structures, often with spinules. A ventral view of the right half of a petasma typical of *Solenocera* species is shown in Fig. 1D.

*Appendix masculina.* This is formed from the endite of the 2nd male pereopod (Fig. 13E). In the Solenoceridae there are outer and inner projections, sometimes distinguished as the appendix masculina and appendix interna, respecively. As the homology of the inner projection is unknown, in this text they are both referred as the appendix masculina. There is also a spur-like projection on the outside of the base of the appendix masculina.

*Thelycum.* This is developed on the sterna of the 4th and 5th female pereopods, the spermatophore being implanted on the latter. It is often a quadrangular depression, usually with various internal projections, but occasionally almost featureless and sometimes a convex projection (Figs 13C, 19D). In some species, the features of the thelycum are variable and difficult to interpret and of limited use in the separation of species.

*Length.* Overall length is difficult to measure accurately in penaeids and often the rostrum and telson are damaged. In this text length is the carapace lenth, i.e. the distance between the posterior rim of the orbit and the posterior rim of the carapace on the midline.

## Family SOLENOCERIDAE
## (Wood, Mason & Alcock, 1891)

Solenocerinae: Wood, Mason & Alcock, 1891; Crosnier 1979

DIAGNOSIS. Rostrum laterally compressed, usually shorter than the antennular peduncle, mostly with dorsal teeth only and more than three; ventral teeth if present, restricted to the tip. Antennular flagella usually longer than the peduncle, often longer than the carapace. Prosartema variable, usually prominent, sometimes reduced to a small lobe; ocular scale present, sometimes poorly developed. Cervical sulcus well defined, reaching or nearly reaching the mid-dorsum of the carapace. A postorbital spine (sometimes called postantennal spine) and hepatic spine are always present; antennal spine usually present, other carapace spines variable. Abdomen wholly or partially carinated. Telson with two fixed sub-apical spines, occasionally with moveable lateral spines as well; very rarely without spines at all. Exopods present on thoracic somites 1-7, in some genera on 8 as well; those on the pereopods sometimes reduced. Petasma tubular and simple; appendix masculina with two endites and with a projection on the outer side of the basal segment; thelycum open, often a simple basin shape. Pleurobranchs on thoracic somites 3-8; usually a single arthrobranch, but sometimes two, which may be small or rudimentary on somite 1; two well-developed arthrobranchs on somites 2-7; a podobranch on somite 2, except in *Haliporus* where they are on 2 and 3, sometimes with very small or rudimentary podobranchs on 4-6; epipods on 1-7.

Diagnostic features of the family are the presence of a post-orbital spine, cervical sulcus reaching to or almost to the mid-dorsum, the long antennular flagella and a spur-like projection on the outer side of the basal segment of the appendix masculina. Most inhabit the outer continental shelf down to several hundred metres, with a few occurring at over 1,000m.

The family is comprised of nine genera: *Cryptopenaeus* de Freitas 1979; *Gordonella* Tirmizi 1960; *Hadropenaeus* Pérez Farfante 1977; *Haliporoides* Stebbing 1914; *Haliporus* Bate 1881; *Hymenopenaeus* Smith 1882; *Mesopenaeus* Pérez Farfante 1977; *Pleoticus* Bate 1888; *Solenocera* Lucas 1850. Most inhabit offshore waters, ranging from the middle continental shelf to the oceanic floor, but a few (*Pleoticus muelleri* and *Solenocera* spp.) are found in shallower waters. The key which follows includes all known genera of the Solenoceridae. Three *Pleoticus* spp. are known, of which two are abundant in the W Atlantic; the third, *P. steindachneri* has been recorded only in the deeper waters of the Red Sea (Crosnier 1988). As *Pleoticus* is not otherwise represented in the Indo-West Pacific, it is not dealt with further.

## KEY TO THE GENERA OF THE SOLENOCERIDAE

1. Telson with three widely spaced pairs of moveable spines, which may be minute, anterior to a sub-apical fixed pair; with an accessory branchiocardiac carina dorsal to the sulcus . . . . . 2

   Telson with a single pair of fixed sub-apical spines only, or with none; without an accessory branchiocardiac carina . . . . . 3

2. Mid-dorsum deeply indented at its junction with the cervical sulcus; with a supra-hepatic (postcervical) spine. A podobranch on the 2nd thoracic somite only . . . . . *Gordonella*

   Mid-dorsum with a shallow depression only in the region of the cervical sulcus; supra-hepatic spine absent. Podobranchs on at least the 2nd and 3rd thoracic somites . . . . . *Haliporus*

3. Dorsal and ventral antennular flagella lamellate and forming a respiratory tube; external ramus of uropod without a distolateral spine . . . . . *Solenocera*

   Dorsal and ventral antennular flagella not forming a respiratory tube, but with the ventral flagellum sometimes flattened; external ramus of uropod with a distolateral spine . . . . . 4

4. Ventral antennular flagellum strongly compressed proximally, orbital spine well developed . . . . . *Mesopenaeus*

   Ventral antennular flagellum more or less cylindrical, orbital spine absent or only a weak orbital angle present . . . . . 5

5. Epigastric tooth separated from the 1st rostral tooth by an interval not markedly different from that between the 1st and 2nd rostral teeth. . . . . 6

   Epigastric tooth, or epigastric tooth and 1st rostral tooth separated from the remaining teeth by a relatively long interval . . . . . 8

6. Rostrum low, with ventral margin straight or concave; submarginal carina present . . . . . *Pleoticus*

   Rostrum deep, with ventral margin markedly convex; submarginal carina absent . . . . . 7

7. Pterygostomian spine present, branchiostegal spine absent; postrostral carina well defined and almost reaching the posterior rim of the carapace . . . . . *Cryptopenaeus*

   Branchiostegal spine present, pterygostomian spine absent; postrostral carina not extending much beyond the top of the cervical sulcus . . . . . *Hadropenaeus*

8. Post-cervical (supra-hepatic) spine absent. Epigastric and 1st rostral tooth separated from the remaining teeth by a relatively long interval . . . . . *Hymenopenaeus*

   Post-cervical (supra-hepatic) spine present Epigastric tooth separated from the 1st rostral tooth by a relatively long interval . . . . . *Haliporoides*

### **Cryptopenaeus** de Freitas, 1979

*Cryptopenaeus* de Freitas, 1979; Pérez Farfante & Kensley, 1997.

DIAGNOSIS. Carapace and abdomen robust, integument firm, mostly glabrous or minutely punctate. Rostrum short, not exceeding the 2nd antennular segment, ventral margin convex, tip horizontal or slightly upturned; with dorsal teeth only, the distance between the epigastric and 1st tooth similar to that between the 1st and 2nd. Antennal, postorbital, hepatic and pterygostomian spines present. Cervical sulcus deep, but not reaching the mid-dorsum; hepatic sulcus deep and long, the anterior end almost reaching the base of the pterygostomian spine; hepatic carina well defined; orbito-antennal sulcus shallow and wide. A dorsal carina on abdominal somites 2-6. Telson with a pair of short fixed sub-apical spines, no moveable lateral spines. Eye of medium size and reaching the tip of the 1st segment of the antennular peduncle; a foliaceous prosartema present, extending beyond the eye. Antennular flagella similar, cylindrical and long. Mandibular palp two-segmented, the segments subequal in length, the distal narrower than the basal and tapering to a rounded apex. Exopods on all thoracic appendages.

Petasma with ventrolateral lobule distally free from the dorsolateral lobule; both with firm integument; right and left petasmal halves united by cincinnuli only for about the proximal half of their length. Thelycum simple, open.

This genus at present includes four species, all rather similar, attaining a large size (over 50mm) and inhabiting depths of 200-500m.

## KEY TO THE SPECIES OF *CRYPTOPENAEUS*

1. Anterior end of hepatic carina strongly recurved ventro-posteriorly . . . . . *C. clevai*

   Anterior end of hepatic carina not recurved . . . . . 2

2. Postrostral carina with a shallow notch behind the level of the top of the cervical sulcus; a spine on the basis of the 3rd pereopod . . . . . *C. catherinae*

   Postrostral carina without such notch; no spine on the basis of the 3rd pereopod . . . . . 3

3. Scaphocerite exceeding the tip of the antennular peduncle by about 0.25 its own length; sternite of 5th female pereopod with two rounded anterior prominences . . . . . *C. crosnieri*

   Scaphocerite about as long as the antennular peduncle; sternite of 5th female pereopod with a single rounded anterior prominence . . . . . *C. sinensis*

*C. clevai* and *C. crosnieri* have been collected from Australian waters; *C. sinensis* has been recorded from NW Australia (Pérez Farfante & Kensley, 1985), but the figures of the petasma and appendix masculina appear to be those of *C. clevai*; *C. catherinae* appears to be endemic to E Africa (off Mozambique). All of these species are uncommon at present.

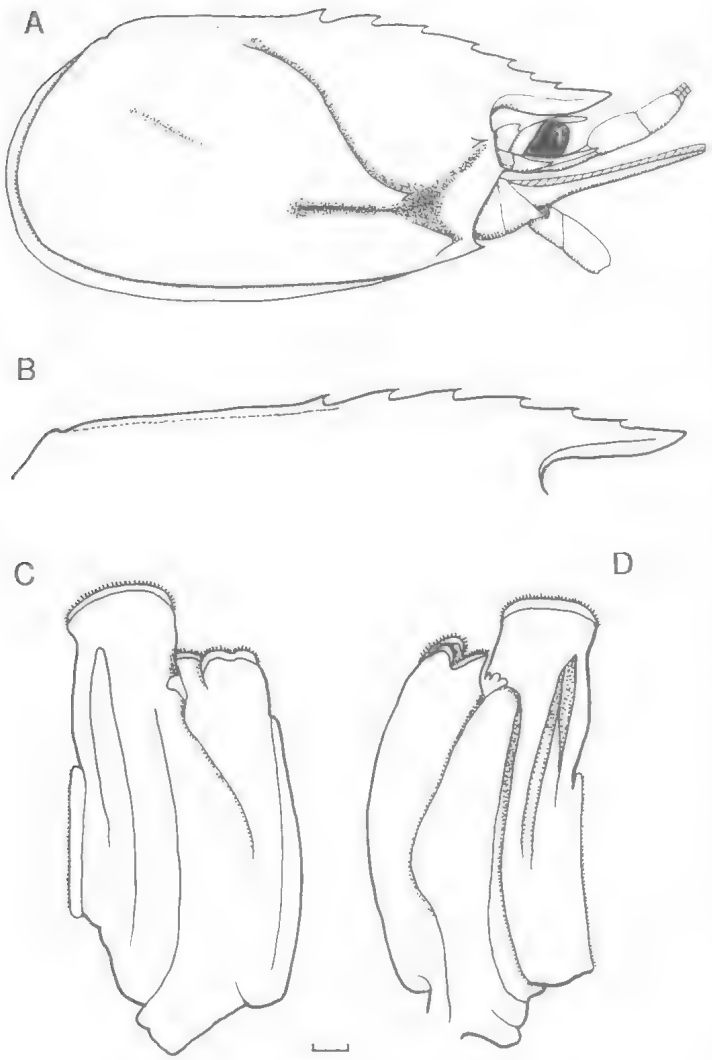



FIG. 2. *Cryptopenaeus clevai* Crosnier, 1984. A, F, 45mm, WAMC24250, 12°51'S 118°25'E, 449m. B, M, 35mm, profile of carapace dorsum. C, ventral left half of petasma, male 40mm WAMC21408, 17°S 119°28'E, 435m. D, dorsal left half of petasma, WAMC21408. (Scalebar = 1mm)

**Cryptopenaeus clevai** Crosnier, 1984
(Fig. 2A-D )

*Cryptopenaeus clevai* Crosnier, 1984: 26-31, figs 1a-b, 2, 3a; 1994b.
*Cryptopenaeus sinensis* Pérez Farfante & Kensley, 1985.

MATERIAL: NTCR007064, F, 56.5mm; WAM21396, F, 64mm; 21398, M, 38.5mm, F, 53.5mm; 21401, F, 55mm; 21408 4M, 40-42mm; 24250 2M, 35, 36mm, 3F, 26, 43, 47.5mm

DIAGNOSIS: Rostrum with 6-7 teeth including the epigastric and reaching the middle of the 2nd segment of the antennular peduncle; four teeth on the carapace. Upper rostral profile sigmoid with the highest point at the 1st rostral tooth, descending to the orbital margin and then ascending towards the tip, the general appearance markedly 'humpbacked' in large specimens, less so in those below 40mm length (Fig. 2B). Postrostral carina prominent, almost reaching the posterior edge of the carapace and without a depression or notch. Carapace glabrous; orbital angle almost absent; antennal and pterygostomian spines small, postorbital and hepatic spines prominent. Anterior end of hepatic carina recurved ventroposteriorly; hepatic sulcus deep; cervical carina prominent, the carina and sulcus ending well short of the dorsal midline. Branchiocardiac sulcus well defined and occupying the middle third of the branchial region. Prosartema reaching 0.3 of the 2nd antennular segment; scaphocerite exceeding the tip of the antennular peduncle by about 0.25 its length. First pereopod with large spines on the basis and ischium and a small spine midway along the merus; 2nd pereopod with a spine on the basis only; no spines on the 3rd pereopod.

*Petasma* (Fig. 2C,D). Distal end of the dorsolateral lobule flattened and fringed with minute spinules; recurved laterally with four small backwardly directed teeth; distal ventro-lateral lobule divided distally, one broad with a slight distal indentation, the other acute and both fringed with minute spinules.

*Colour.* Deep pink to red with whitish markings, rostrum bluish.

REMARKS. The Western Australian Museum has a large collection of this species, which has often been trawled at around 450m depth.

DISTRIBUTION. NW Australia, 390-450m. Known range, Indonesia (type locality), Japan, Taiwan, N Australia, New Caledonia, Wallis and Futuna I., 300-540m

### **Cryptopenaeus crosnieri**
Pérez Farfante & Kensley 1985
(Fig. 3)

*Cryptopenaeus crosnieri* Pérez Farfante and Kensley 1985: 280-287, figs 1-4.

MATERIAL: QMW15825, 2 F, 35, 40mm; 15826, M, 33.5mm [allotype]; 15839, 2 F, 42, 44mm; 16214, F, 49mm; 16222, 2 F, 45.5, 46.5mm.

DIAGNOSIS. Dorsal rostral margin convex, rostral teeth including epigastric 7-9 , usually 8, the rostrum reaching about the distal end of the 1st segment of the antennular peduncle in adults. Postrostral carina well-defined, almost reaching the posterior border of the carapace and without a notch or depression. Postorbital and hepatic spines large and slender, antennal and pterygostomian spines smaller. Hepatic carina ending beside a shallow, elongate depression which extends towards the pterygostomian spine; branchiocardiac sulcus extremely faint. Prosartema long and narrow and reaching almost half the 2nd antennular segment. Antennular flagella subequal in length and 1.5-2.0 the length of the carapace; scaphocerite exceeding the antennular peduncle by up to 0.25 its length. First pereopod with a prominent basial spine, a similar ischial spine and a small spine about halfway along the ventral edge of the merus; a large basial spine on the 2nd pereopod. Abdomen with a low dorsal carina on the posterior half of the 2nd somite; carina becoming sharp on the 4th to 6th.

Fifth thoracic sternite of female with a subrectangular plate with a deep longitudinal groove on each side, each with a strong lateral ridge joined anteriorly by a transverse ridge; coxa of 5th pereopods produced inwards in a plate bearing an anteriorly-directed spine; sternite of 4th pereopods with a prominent median ridge with a large blunt anterior tooth.

REMARKS. Pérez Farfante & Kensley (1985) state that there is a 'very minute' spine on the merus of the 3rd pereopod in this species, but no such spine could be found on the above specimens.

Colour predominantly deep pink to red with whitish markings (Crosnier, 1994b)

DISTRIBUTION. NW Australia, E Australia 16°-30°S, 230-440m. Known range, Kai I. (Indonesia), N Australia.

### **Gordonella** Tirmizi, 1960

*Gordonella* Tirmizi, 1960: 372; Crosnier, 1988 (emend): 586-587; Pérez Farfante & Kensley, 1997.

DIAGNOSIS. Integument soft, with prominent accessory lateral carinae on the carapace and abdomen, which appear to reinforce it. Rostrum straight, sharply tapering and slightly upturned, with dorsal teeth only and not exceeding the 2nd segment of the antennular peduncle. Distance between the epigastric tooth and 1st rostral tooth similar to that between the remaining teeth. Cervical sulcus ending in a deep notch in the dorsum; carapace strongly convex behind this notch. Antennal, postorbital, suprahepatic (postcervical), hepatic and pterygostomian spines present. Abdomen relatively slender, with dorsal carinae on all somites. Telson pointed apically, with a pair of sub-apical spines and with three pairs of small widely spaced moveable spines on the lateral border. Eye small and fully pigmented, ocular scale reduced, stylocerite poorly developed. Antennular flagella identical, cylindrical, filiform and very long. Mandibular palp 3-segmented, the distal segment slender; incisor process of the mandible long and entire; molar process small. Exopods on all thoracic appendages, those on the pereopods very small.

This genus was originally erected by Tirmizi (1960) to include what was mistakenly thought to be a new species, *G. polyarthra,* but which turned out to be a poorly preserved specimen of *Haliporus villosus* Alcock & Anderson, 1894. However, this species is sufficiently different from other species of *Haliporus* to warrant the

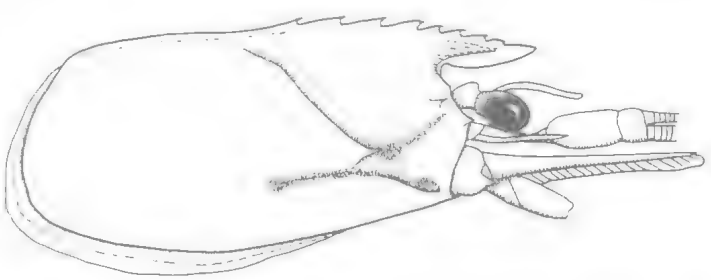


FIG. 3. *Cryptopenaeus crosnieri* Pérez Farfante & Kensley, 1985. QMW15825, F, 35mm, 28°11'S 153°54'E, 230m.

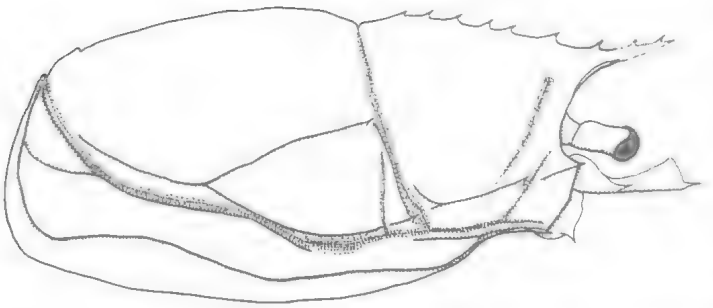


FIG. 4. *Gordonella paravillosa* Crosnier, 1988. QMW00456, F (paratype), 47.5mm, 17°45'S 148°01'E, 1,147-1,132m.

retention of the genus, which has been fully redefined by Crosnier (1988), and now includes three species, all from the Indo-West Pacific. *Gordonella* has close affinities with *Haliporus*, and the species of both genera have rarely been caught at depths less than 750m, most inhabiting the 1,000-6,000m range.

Only three species, all rather different in appearance from most other solenocerids, are included in this genus.

KEY TO THE SPECIES OF *GORDONELLA*
(after Crosnier, 1988)

1. Integument entirely covered by a dense, short pubescence . . . . . 2
   Integument glabrous . . . . . *G. kensleyi*
2. Prosartema absent . . . . . *G. paravillosa*
   Prosartema present . . . . . *G. villosa*

The type locality of *G. kensleyi* Crosnier, 1988 is New Caledonia, but it has also been collected from 2,450m on the Lord Howe Rise (A. Crosnier pers. com.) and thus could be considered to be an Australian species as well as *G. paravillosa*. It has not been described and figured here as no specimens were available. *G. villosa* is known only from the Indian Ocean and may be present off Western Australia. *Gordonella* species appear to be uncommon, if not rare, but this apparent rarity may be due to their habitat depths, which are rarely fished.

**Gordonella paravillosa** Crosnier, 1988
(Fig. 4)

*Gordonella paravillosa* Crosnier, 1988: 589, figs 2d, 3c, 12a, 13, 14, 15a-e, 16a-f

MATERIAL: QMW13224, F, 47.5mm, paratype.

DIAGNOSIS. Cephalothorax bulbous in profile, abdomen relatively slender with long pleopods. Cuticle of the carapace thin and flexible and covered with setae. Rostrum upturned, exceeding the eye, teeth fairly evenly spaced, the 1st smaller than the others or vestigial; adrostral carina short; postrostral carina extending almost to the posterior edge of the carapace, a small tubercle towards the posterior end. No orbital angle; post-orbital spine post-antennal in position; post-orbital, antennal, hepatic, suprahepatic, pterygostomian spines present and of similar size; spines and carinae sharp. A short antennal carina present and an orbito-antennal sulcus running below the postorbital spine to its junction with the hepatic sulcus. Postorbital spine extended posteriorly in a carina, interrupted by the cervical sulcus. A postorbital sulcus running parallel to the orbital margin from the base of the rostrum to the carina behind the postorbital spine. Hepatic carina extending posteriorly from the pterygostomian spine to the level of the base of the hepatic spine; hepatic sulcus extending from its junction with the orbito-antennal sulcus to its junction with the branchiocardiac sulcus. The latter deep and reaching the posterior mid-dorsum; branchiocardiac carina prominent and with an accessory parallel carina on its dorsal side, which ends at a small vertical sulcus just behind the hepatic spine; suprahepatic spine with a carina which extends posteriorly to meet the latter. Marginal carina well defined, running from its juction with the hepatic carina to the posterior mid-dorsum of the carapace. Cervical sulcus deep and interrupting the postrostral carina with a deep cleft; cervical carina extending from the suprahepatic spine to the hepatic spine. Eye small; prosartema absent; antennular flagella cylindrical and longer than the carapace. Abdomen dorsally and mid-laterally carinated on all six somites; telson with a pair of fixed sub-apical spines and three pairs of mobile lateral spines. Thelycal plate of the 4th pereopods subtriangular, apex facing posteriorly, that of the 5th pereopods similar but markedly larger.

REMARKS. Because of the very soft and flexible cuticle, there tends to be some distortion of preserved specimens, making interpretation of features of the carapace difficult. However, Fig. 4, taken from a paratype, agrees closely with that of the holotype (Crosnier, 1988, fig. 12a). The missing tip of the rostrum in the paratype was taken from this figure. Crosnier records the

length of the this paratype as 43mm, presumably a typographical error, as it was found to be 47.5mm.

*G. paravillosa* is similar to *G. villosa*, but as the holotype is poorly preserved and damaged, the only reliable means of separating the two species at present is by the key feature i.e. the lack of a prosartema on the antennular peduncle.

The long pleopods and thin cuticle suggest that *G. paravillosa* is at least partly pelagic.

DISTRIBUTION. Indonesia (Celebes region, 1280 m), off NE Queensland, 17-18°S 148°E, 1147-1200m (type locality), and New Caledonia (A. Crosnier, pers. com.)

### **Hadropenaeus** Pérez Farfante, 1977

*Hadropenaeus* Pérez Farfante, 1977: 315-316; Pérez Farfante & Kensley, 1997.

DIAGNOSIS. Body fairly robust, integument firm, rostrum short, not exceeding 1/3 of the 2nd segment of the antennular peduncle, with dorsal teeth only, the distance between the epigastric and 1st rostral tooth similar to that between the 1st and 2nd teeth. Orbital and pterygostomian spines absent; postorbital, antennal, hepatic and branchiostegal spines well defined. Cervical sulcus almost reaching the middorsum; hepatic sulcus present; branchiocardiac carina absent, sulcus barely defined or absent. Abdomen dorsally carinated on 3rd to 6th somites. Telson with a pair of fixed sub-apical spines, without lateral moveable spines. Prosartema foliaceous and reaching at least as far as the eye. Antennular flagella longer than the carapace, subcylindrical, rarely with the ventral flagellum slightly flattened. Mandibular palp 2-segmented, the two subequal in length, the distal segment tapering to a blunt apex. First pereopod with a spine on the basis, ischium and merus. Fifth pereopod slender and much longer than the 4th. Epipods on all thoracic somites. Outer ramus of the uropod with a distolateral spine reaching as far as the lamella of the uropod. Petasma with terminal part of the ventrolateral lobe plate-like with thickened cuticle; ventromedian lobule broadly expanded distally. Basal sclerite of appendix masculina produced into an elongate ventrolateral spur. Thelycum of open type, not enclosing a seminal receptacle.

This genus so far contains only four species, of which two are from the Atlantic; all are similar in general appearance and have been recorded from the 100-600mdepth range, but more usually 200-500m.

### KEY TO THE INDO-WEST PACIFIC SPECIES OF *HADROPENAEUS*

Dorsal carina of 6th abdominal somite without lateral moveable spines, posterior margin of somite not crenate. Rostrum with a small accessory adrostral carina just below the bases of the teeth . . . . . *H. lucasii*

Dorsal carina of 6th abdominal somite with 4 lateral moveable spines on either side, posterior margin of somite crenate. Rostrum without an accessory adrostral carina . . . . . *H. spinicauda*

Of the two Indo-West Pacific species only *H. lucasii* has been recorded from Australia.

### **Hadropenaeus lucasii** (Bate 1881) (Fig. 5)

*Solenocera lucasii* Bate, 1881: 185.
*Philonicus lucasii* Bate, 1888.
*Pleoticus lucasii* Bate, 1888.
*Haliporus modestus* Rathbun, 1906.
*Haliporus lucasi* Bouvier, 1908.
*Haliporus lucasii* de Man, 1911.
*Hymenopenaeus lucasii* Burkenroad, 1936; Anderson & Lindner, 1945; Kubo, 1949.
*Hymenopenaeus lucasi* Crosnier & Forest, 1973; Crosnier, 1978.
*Hadropenaeus lucasi* Crosnier, 1984, 1989, 1994a,b; Kensley,Tranter & Griffin, 1987.
*Hadropenaeus lucasii* Pérez Farfante, 1977; Hayashi, 1984b,c.

MATERIAL. QMW15876, F, 8mm; 15877, F, 7.5mm. 2M, 7.5, 8mm; 158028 M, 7.5mm; 15888, F, 21mm; 15898, 3F, 13.5, 14.5, 20mm; 16205, M, 20mm.

DIAGNOSIS. Carapace almost entirely glabrous, with some pubescence in the rostral area; abdomen glabrous. Rostral upper edge straight and almost horizontal, teeth prominent, ventral margin convex; rostral teeth, including epigastric 6-8, mostly 7; 3rd rostral tooth around the level of the orbital margin; rostrum reaching about as far as

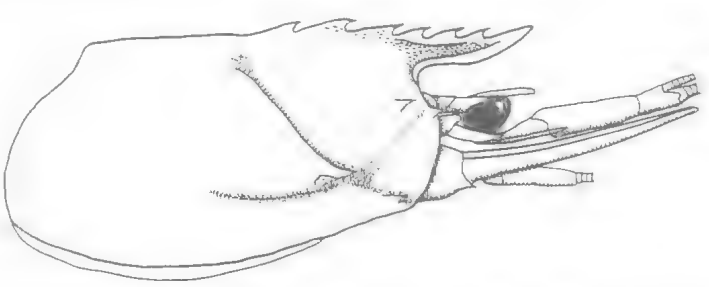


FIG. 5. *Hadropenaeus lucasii* (Bate, 1881). QMW15888, F, 21mm, 27°55'S 154°E, 555m.

the 1st segment of the antennular peduncle. Adrostral carina reaching the last rostral tooth; an accessory carina extending from the base of the 2nd to the penultimate rostral tooth, the two carinae enclosing a shallow, setose channel; postrostral carina ending just behind the level of the cervical sulcus. Orbital angle absent, but the lower orbit extended into a short inwardly-directed shelf. Hepatic carina absent, the sulcus shallow, inclined anteroventrally and ending in a depression below the prominent branchiostegal spine. Prosartema exceeding the eye; antennular flagella long and of unequal length. First pereopod with long spines on the basis and ischium, a smaller spine at the mid-length of the merus; a long spine on the basis of the 2nd pereopod; in both sexes coxa of the 4th and 5th pereopods with conspicuous antero-median spines. Abdomen with a well-developed dorsal carina on the 3rd to 6th somites, rounded on the 3rd, keel-like on the 4th to 6th. (For description of petasma and thelycum see Pérez Farfante, 1977; Crosnier, 1978).

REMARKS. Rostrum blue; carapace red to light pink, with whitish patches; abdomen with vertical bands of red, lighter colour between; uropods similarly banded, other appendages red.

DISTRIBUTION. N Australia and E Australia 17°-28°S, 300-590m. Known range, Madagascar through the Indian Ocean and W Pacific, Japan to Hawaii and Wallis and Futuna Is, 180-600m. The type locality is the Kai I. and *H. lucasii* has recently been collected here and also further south in the Arafura Sea (Crosnier 1994a). The collections off E Australia further extends the range of this species.

### **Haliporoides** Stebbing, 1914

*Haliporoides* Stebbing 1914: 20; Pérez Farfante & Kensley, 1997.

DIAGNOSIS. Carapace elongate, integument flexible; rostrum exceeding the middle of the 2nd segment of the antennular peduncle, with dorsal teeth and often with ventral rostral teeth towards the tip, ventral margin straight or concave; the interval between the epigastric tooth and the 1st rostral teeth appreciably greater than that between the remaining teeth. Postorbital, antennal, pterygostomian, hepatic and supra-hepatic (postcervical) spines present; orbital and branchiostegal spines absent. Cervical sulcus reaching the mid-dorsum but not incising it; hepatic sulcus long, reaching or almost reaching the base of the pterygostomian spine; orbito-antennal and branchiocardiac sulci clearly defined; a sharp submarginal carina present. Eye large, maximum length 0.2 or more the length of the carapace. Antennular flagella similar in length, subcylindrical and three times or more the length of the carapace. Mandibular palp 3-jointed, 4th and 5th pereopods of similar length, 1st pereopod with or without a basial spine; small exopods on all pereopods and maxillipeds. Pleopods large in relation to the pereopods, suggesting that the genus is at least partly natatory.

#### KEY TO THE INDO-WEST PACIFIC SPECIES OF *HALIPOROIDES*

1. Rostrum with 6-8 dorsal teeth plus epigastric and 1-2 ventral teeth, slender and slightly down-curved or straight . . . . . *H. sibogae*

   Rostrum with 10-11 dorsal teeth plus epigastric, blade either very high and strongly down-curved, or high with slightly upcurved tip . . . . . 2

2. Rostral blade very high and down-curved with 1-2 ventral rostral teeth. . . . . *H. triarthrus*

   Rostral blade high, arched behind the 1st ventral rostral tooth and slightly upcurved at the tip; 2-4, usually 3 ventral rostral teeth. . . . . *H. cristatus*

These three species are similar in appearance and overlap in some of their features e.g. rostral teeth. *H. sibogae* is particularly variable and two subspecies have been named:

*H. sibogae madagascarensis* Crosnier, 1978 and *H. sibogae australiensis* Kensley, Tranter & Griffin, 1987. The latter authors found that all the Australian specimens examined belonged to this subspecies. *H. triarthrus* also includes a subspecies, *H. t. vniroi* (Crosnier, 1978). These subspecies do not key out satisfactorily and are best identified by a table (Kensley et al., 1987).

Of the three *Haliporoides* species *H. sibogae* and *H. triarthrus* are commercially abundant, while *H. cristatus* appears to be fairly common.

### **Haliporoides cristatus** Kensley, Tranter & Griffin, 1987 (Fig. 6A)

*Haliporoides cristatus* Kensley, Tranter & Griffin, 1987: 265, figs 1, 2, 5G-L.

MATERIAL: QMW11285, 2F, 23, 23mm; 14288, M, 17.5mm; 14308, M, 20mm, F, 18mm; 15857, F, 27.5mm; 15889, 3M, 17.5, 19, 19mm; 5F, 17, 18, 20, 20.5, 21mm; 15895, F, 25mm; 15902, F, 28mm; 16216, F, 32mm; 16212, F, 34mm.

DIAGNOSIS. Carapace and abdomen finely punctate-setose. Rostrum arched, deep and often

upturned at the tip, reaching from two thirds to the tip of the 2nd segment of the antennular peduncle; with 8-12 dorsal teeth, including the epigastric, and 2-4 ventral teeth (mean 10/3). Adrostral carina prominent; a lower but distinct accessory adrostral carina below the upper rostral teeth. Postrostral carina ending about halfway between the tip of the epigastric and the top of the cervical sulcus. Antennal, postorbital and pterygostomian spines of similar size and larger than the hepatic and supra-hepatic spines, which are also of similar size to one another. A short antennal carina and a shallow orbito-antennal sulcus present. Hepatic carina short; anterior part of the hepatic sulcus shallow, running from the anterior margin of the carapace to the base of the hepatic spine and continuing, slightly deeper, for a similar distance posteriorly. Branchiocardiac sulcus fairly shallow and extending from just behind the end of the hepatic sulcus almost to the posterior margin of the carapace; branchiocardiac carina not defined. Cervical sulcus deep and reaching the dorsum; cervical carina blunt and not prominent; submarginal carina sharp. Prosartema reaching as far as the eye. No spine on the basis of the 1st pereopod. Other features, including the petasma and thelycum as described by Kensley et al. (1987).

REMARKS. Although the carapaces of *H. sibogae* and *H. cristatus* are similar, the rostral shape and number of teeth are quite different. In the field or with fresh specimens, colour may enable quick provisional identifications to be made, but this needs to be verified.

Colour yellowish, with a distinctive white stripe on the dorsal surface of the uropods.

DISTRIBUTION. So far collected only from E Australian waters, from 16°-35°30'S, 250-650m.

**Haliporoides sibogae** (de Man, 1907)
(Fig. 6B)

*Haliporus sibogae* de Man, 1907: 38; 1911: 7.38; 1913, pl 3, fig. 10a-b, pl. 4, fig. 10c-q.
*Haliporoides sibogae* Pérez Farfante, 1977; Crosnier, 1984, 1989, 1994; Grey, Dall & Baker, 1983; Hayashi, 1984b.
*Haliporoides sibogae australiensis* Kensley Tranter & Griffin, 1987: 269, figs 3-5.
*Hymenopenaeus sibogae* Crosnier, 1978.
*Parahaliporus sibogae* Kubo, 1949.

MATERIAL. QMW15882, 2F, 24, 38.5mm; 15887, 5M, 23.5, 23.5, 24.5, 25.5, 30mm; 15890, 2M, 26, 27mm; 15901, F, 29mm; 15917, 3F, 27, 35, 35.5; 16213, F, 35mm; 16216, F, 32mm; WAMC16930, M, 36mm, F, 37mm; 21400, 2F, 36, 42mm; 21409, 2M, 32, 40mm, F, 50mm; 25275, 2M, 28, 31mm; 25276, F, 19mm; 25277, M, 30mm, 2F, 28, 29mm; 25278, M, 27mm; 25279, M, 29mm; 25280, F, 39mm; 25281 F, 31mm; 25283, 2F, 36, 38mm; 25284, F, 38mm; 25285, 2F, 30, 38mm; 25286, F, 40mm; 25287, F, 40mm; 25288, 2M, 22, 30mm, 4F, 37, 38, 39, 40mm.

DIAGNOSIS. Cuticle flexible, carapace finely punctate-setose. Rostrum ascending from the carapace and then down curving slightly; reaching from half the 2nd segment of the antennular peduncle to its tip; teeth 7-9, usually 8 dorsal, including the epigastric, and 1-2 ventral. Postrostral carina ending about half way between the tip of the epigastric tooth and the top of the cervical sulcus. Orbital angle absent, antennal and postorbital spines of equal size and larger than the remaining spines, the postorbital behind the antennal. Hepatic, suprahepatic and pterygostomian spines of similar size. Cervical sulcus deep and almost reaching the mid-dorsum. Hepatic carina short, not strongly defined and extending towards the tip of the pterygostomian spine; the hepatic sulcus fairly shallow anteriorly and reaching from the anterior rim of the carapace to the base of the hepatic spine, where it deepens and extends posteriorly

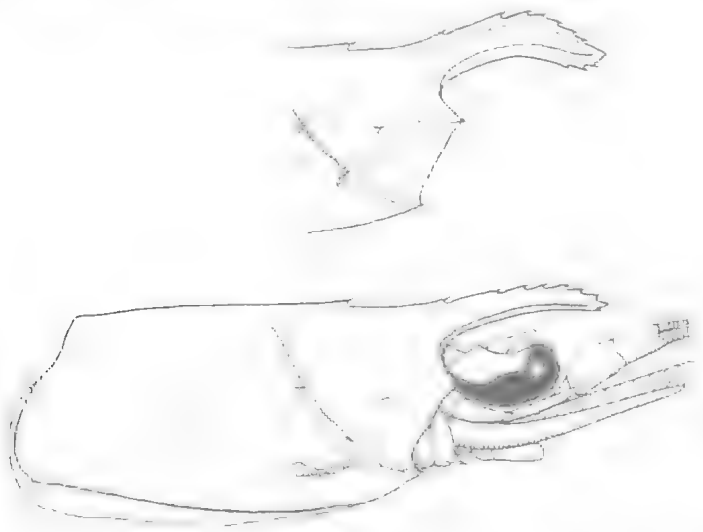


FIG. 6. A, *Haliporoides cristatus* Kensley, Tranter & Griffin, 1975. QMW16212, F, 34mm. 15°58'S 149°56'E, 590m. B, *H. sibogae* (de Man, 1907). QMW15917, F, 34.5mm, 23°35'S 153°20'E, 650m.

for a similar distance. A shallow orbito-antennal sulcus present. Branchiocardiac sulcus well defined, almost meeting the hepatic sulcus and almost reaching the posterior rim of the carapace; branchiocardiac carina not sharply defined. Sub-marginal carina sharp. Prosartema not quite reaching as far as the eye. No spine on the basis of the 1st pereopod. Ventro-median lobe of the petasma tapering to a blunt point, sometimes curved, sometimes almost straight. Sternite of the female 5th pereopod without a longitudinal ridge.

REMARKS. Kensley et al. (1987) considered that there were sufficient differences in the eastern Australian specimens to warrant the erection of a new subspecies *H. sibogae australiense*. Their justification for this was the length of the postrostral carina, the size of the suprahepatic spine relative to the hepatic spine, the absence of a longitudinal ridge on the sternite of the female 5th pereopod, the ventromedian lobule of the petasma not distally bent, the zygocardiac ossicle structure and slight differences in the appendix masculina. They found that these features were consistent for all of the Australian specimens examined. However, the Queensland Museum specimens, while agreeing with the *H. sibogae australiense* criteria, also agree closely with both de Man's (1913) figures and Crosnier's (1978) description and figures of the syntype of *H. sibogae* . An exception is the lack of a longitudinal ridge on the female sternite, but even here de Man (1913) figures a thelycum where it is absent and states that in the holotype it is 'faintly carinate'. The figure in Liu & Zhong (1986) is small, but no ridge is shown. Examination of the 10 males and 20 females from the Western Australian Museum, collected from the northwestern region of Australia showed that 4 of the criteria used by Kensley et al. (1987) are unreliable as distinguishing features. The hepatic and suprahepatic spines were variable in size and in only 60% were they of similar size; the extent of the postrostral carina was variable and dependent on the interpretation of 'carina', but in 40% of cases could be said to reach as far as the cervical sulcus; the shape of the thelycal plate on the female 5th pereopods varied from a slight convexity to a round hump or a broad longitudinal ridge and in one case could be said to be 'faintly carinate'; the distal end of the ventromedian lobe of the petasma was curved in three cases and bent in one. The NW Australian specimens could be expected to be closely similar to the type specimens from Indonesia, with consistent differences distinguishing them from the E Australian subspecies, but such differences do not appear to exist and the status of *H. sibogae australiens* is thus very doubtful.

Colour is uniformly red-pink to bright red.

DISTRIBUTION. E Australian coast from 16°-40°S, NW Australia; 350-900m. Fished commercially off E Australia and known as the Royal Red Prawn. Known range, Madagascar to Indonesia, South China Sea, Japan, Australia and New Zealand, 100-900m.

### **Haliporus** Bate, 1881

*Haliporus Bate*, 1881: 85; 1888: 284; Crosnier, 1988; Pérez Farfante & Kensley, 1997.

DIAGNOSIS. Body glabrous or pubescent, integument soft or firm. Abdomen with lateral carinae; carapace moderately deep. Rostrum variable in length and shape, no ventral teeth; distance between the epigastric tooth and 1st and 2nd teeth not markedly different. Antennal, postorbital, hepatic and pterygostomian spines present. Branchiocardiac sulcus deep, the carina prominent; with an accessory carina above and parallel to the sulcus. Cervical sulcus deep and with a large depression at the dorsum of the carapace. All abdominal somites with a dorsal carina, with or without a terminal tooth. Telson with a pair of small fixed sub-apical spines, and with three pairs of widely spaced mobile spinules, which may be minute. Eye small, maximum diameter 0.09 the length of the carapace or smaller; cornea pigmented and much wider than its peduncle, or about the same width as the peduncle and lightly pigmented. Prosartema present, slightly or well developed, never foliaceous. Stylocerite well developed. Antennular flagella identical, cylindrical and filiform and very long. Mandibular palp with three segments, the 1st annular and very short, the 2nd much longer and wide, the 3rd slender and much shorter than the 2nd. Fourth pereopods a little shorter or clearly longer than the 3rd; 5th much longer than all the other pereopods; no pereopods filiform. Exopods on all thoracic somites; that on the 2nd maxilliped attaining or surpassing the extremity of the merus; that of the 3rd small, single or multi-segmented. Outer ramus of uropods with a strong disto-lateral tooth, not as long as the lamellar part. Pleopods long in relation to the thoracic appendages.

Thelycum of open type, without a seminal receptacle. A rounded projection on the sternite

of thoracic sternite 7, a larger one on sternite 8. Petasma symmetrical with simple structure; dorsomedian lobule very short to short, extending for 0.15-0.30 the length of the petasma; ventromedian lobule spatulate, more or less curved at its extremity; dorsolateral lobule distally wide and sinuous; ventrolateral lobule with extremity well detached, sometimes enlarged, weakly or strongly recurved. Appendix masculina triangular in cross section, with two or three of its faces concave and longer than the appendix interna; the latter either subcylindrical or flattened. Base of the endopods of the 2nd pleopods with a large foliaceous expansion, more or less recurved distally.

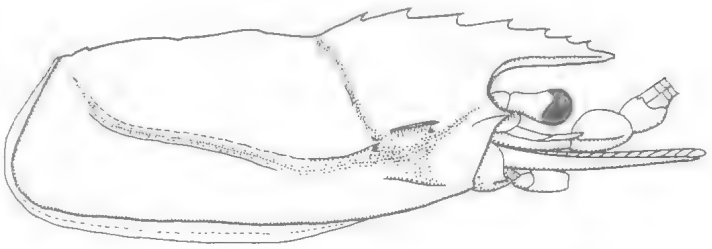


FIG. 7. *Haliporus taprobanensis* Alcock & Anderson, 1899. NTCR006634, F, 53.5mm, 8°38'S 132°E, 525-540m.

Podobranchs always present on somites 2 and 3, sometimes on 4-6 as well, those on 3-6 small to rudimentary.

The above definition is from Crosnier (1988), who revised the genus and its 3 constituent species in detail. These 3 species are included in the following key, also from Crosnier. *H. curvirostris* has so far been collected only from the Pacific at depths between 4,361 and 5,700m; *H. thetis* has been recorded from the Galapagos Is and the Indian Ocean at depths between 2,300 and 3,625m; *H. taprobanensis* appears to live at lesser depths (see below).

## KEY TO THE SPECIES OF *HALIPORUS*

1. Integument soft. Eye not exceeding half the 1st segment of the antennular peduncle, the cornea lightly pigmented and of similar width to its peduncle. Distal part of rostrum down-curved . . . . . *H. curvirostris*

   Integument firm. Eye attaining the tip of the 1st segment of the antennular peduncle, the cornea black and much wider than its peduncle. Rostrum straight or upcurved . . . 2

2. No postero-dorsal spine on the 4th abdominal somite; dorsum of 1st to 4th abdominal somites with numerous pits . . . . . *H. thetis*

   A postero-dorsal spine on the 4th abdominal somite; dorsum of 1st to 4th abdominal somites without numerous pits . . . . . *H. taprobanensis*

### Haliporus taprobanensis
Alcock & Anderson, 1899
(Fig. 7)

*Haliporus taprobanensis* Alcock & Anderson, 1899a: 280; Alcock & Anderson, 1899b; Alcock, 1901; Crosnier, 1978, 1984, 1988, 1994; de Freitas, 1985; Liu & Zhong, 1986.

*Hymenopenaeus taprobanensis* Burkenroad, 1936; Anderson & Lindner, 1945; Burukovsky, 1974.
*Hymenopenaeus kannemeyeri* Kensley, 1977.

MATERIAL. NTCR006634, 5F, 41.5, 49.5, 50, 53.5, 56mm; NTCR006635, 2F, 44.5, 46mm.

DIAGNOSIS. Body robust, integument calcified, carapace glabrous, but minutely punctate in some areas. Rostrum with 7-8 teeth, including the epigastric, shape variable, upper margin convex, lower margin convex to straight, reaching from about 0.6 the 2nd antennular segment to 0.5 the 3rd. Adrostral carina sharp, orbital angle absent. Antennal, postorbital and hepatic spines prominent and of similar size; pterygostomian spine smaller. Orbito-antennal sulcus shallow; hepatic sulcus deep and extending from below the base of the post-orbital spine to its junction with branchiocardiac sulcus; hepatic carina sharp but short, ending below the hepatic spine. Branchiocardiac sulcus deep and curving towards the dorsum of the carapace almost at its posterior margin; branchiocardiac carina blunt and almost the same length as the sulcus. A post-hepatic carina extending from the hepatic spine to the end of the hepatic sulcus, then continuing as a blunt ridge parallel to the branchiocardiac sulcus. Submarginal carina sharp. Cervical carina very short; the sulcus deep, both sides meeting at the dorsum of the carapace; postrostral carina with a wide depression at this point; postrostral carina reappearing behind the cervical sulcus as a short hump, with another depression about halfway from the cervical sulcus to the posterior border of the carapace, after which the postrostral carina reappears again as a lower hump. Dorsal carina of the abdomen beginning on the posterior half of the 1st somite and with a posterior spine on somites 4-6 only. Sub-apical fixed spines on the telson small, the lateral moveable spinules minute. Peduncle of the eye with a small internal nodule; prosartema a rigid vertical projection with a large apical tuft of

setae. First segment of the antennular peduncle with an antero-median spine; stylocerite well defined; lateral carina of the 1st segment continued on the 2nd segment for most of its length. Scaphocerite with a lateral and a median ridge. First pereopod with basial and ischial spines and a moveable sub-apical spine on the merus.

REMARKS. Crosnier (1988) should be consulted for details of the genitalia. This species is similar to *H. thetis*, but appears to have a shallower depth range and thus has been collected more often.

DISTRIBUTION. In Australian waters, so far collected only between 8°38' and 9°17'S, immediately to the north of Darwin (i.e. just inside Australian territorial waters), 300-540m (300m is the shallowest depth recorded). Known range, off South Africa 28°21'S, Madagascar, south of India, Indonesia and the Philippines to N Australia, 300-1650m.

## **Hymenopenaeus** Smith, 1882

*Hymenopenaeus* Smith (1882): 91; Pérez Farfante (1976); Pérez Farfante & Kensley (1997).

DIAGNOSIS. Body fairly slender, cuticle thin; rostrum variable in length, but always well exceeding the eye and acute; usually with only dorsal teeth, the epigastric and 1st tooth separated from the remaining teeth by a longer interval than those between the remaining teeth. Orbital spine absent; postorbital, antennal, hepatic and branchiostegal spines present; pterygostomian spine present or absent. Cervical sulcus deep and reaching the dorsum; branchiocardiac sulcus deep, the carina sharp; posthepatic and submarginal carinae present. Telson with a pair of fixed, prominent sub-apical spines. Antennular flagella similar, cylindrical and longer than the carapace. Mandibular palp 2-segmented, narrow with the distal segment much shorter than the 1st. First pereopod with a spine on the basis and usually on the ischium and sometimes on the merus. Exopods on thoracic somites 1-8. Fourth and 5th pereopods long and extremely slender. External ramus of the uropod with a distolateral spine.

There are seven Indo-West Pacific species in this genus, of which four have been recorded from Australian seas. All species are of similar appearance, mostly small, sometimes difficult to distinguish, and inhabiting the lower continental slope.

### KEY TO THE INDO-WEST PACIFIC SPECIES OF *HYMENOPENAEUS*

1. Pterygostomian spine present . . . . . *H. sewelli*
   Pterygostomian spine absent . . . . . 2
2. Eye small, its greatest diameter <0.12 the length of the carapace . . . . . **H. neptunus*
   Eye medium to large, its greatest diameter 0.15 or more the length of the carapace . . . . . 3
3. Postrostral carina not distinct behind the cervical sulcus 4
   Postrostral carina distinct behind the cervical sulcus and reaching almost to the posterior rim of the carapace . . . . . *H. obliquirostris*
4. Basis and merus of the 1st pereopod each with a ventral spine; scaphocerite about the same length as the antennular peduncle . . . . . *H. halli*
   Basis and merus of the 1st pereopod without spines; scaphocerite exceeding the antennular peduncle by about 0.25 of its length . . . . . 5
5. Rostral teeth usually 8 or 9; eye large, maximum diameter 0.22-0.24 the length of the carapace; distal ventromedian lobule of petasma with two projections; sternum of female 4th pereopods with a prominent glabrous transverse projection . . . . . *H. equalis*
   Rostral teeth usually 7, eye of medium size, maximum diameter 0.15-0.18 the length of the carapace; distal ventromedian lobule of petasma with a single rounded projection with a minute incision; sternum of female 4th pereopods with a rounded setose projection . . . . . *H. propinquus*

* The rare species *H. furici* Crosnier (1978) is very close to *H. neptunus*, but only two males are known, collected from NW Madagascar. For identification see Crosnier (1978).

### **Hymenopenaeus equalis** (Bate, 1888) (Fig. 8A)

*Haliporus equalis* Bate, 1888: 285, pl. 41, fig. 1.
*Haliporus aequalis* de Man, 1911, 1913.
*Hymenopenaeus aequalis* Kubo 1949; George, 1967, 1969; Lee & Yu, 1977; Crosnier, 1985; Hayashi, 1985; Liu & Zhong, 1986.
*Hymenopenaeus equalis* Crosnier & Forest, 1973; Crosnier, 1989, 1994a, b.

MATERIAL. NTCR000627, 2F, 13.7, 14mm.

DIAGNOSIS. Rostrum acute, with ventral margin usually slightly convex, with 7-10 teeth, usually 8 or 9 and reaching from the middle to the tip of the 2nd antennular segment; adrostral carina prominent; postrostral carina becoming indistinct towards the cervical sulcus, with slight indication of a ridge for short distance thereafter. Postorbital and hepatic spines of similar size, antennal spine smaller; branchiostegal spine very prominent, its tip just inside the carapace margin and raised well above its level. Hepatic sulcus beginning at the anterior rim of the carapace, deepening posteriorly and ending in the vicinity of the anterior end of the branchiocardiac sulcus;

TABLE 1. Principal features distinguishing *Hyemnopenaeus equalis*, *H. halli*, *H. neptunus*, *H. propinquus*. * Crosnier (1978, 1989) notes that exceptionally the range may be: *H. equalis* 7-10; *H. halli* 7-9; *H. propinquus* 7-10.

| Feature | *H. equalis* | *H. halli* | *H. neptunus* | *H. propinquus* |
|---|---|---|---|---|
| *Usual number of rostral teeth | 9 | 8 | 6-7 | 7 |
| Ventral margin of rostrum | variable, often slightly convex | usually slightly concave | convex | almost straight |
| Spines on 1st pereopod: | | | | |
| basis | absent | present | present | absent |
| merus | absent | present | present | absent |
| Max. diameter eye/carapace length | 0.22-0.24 | 0.21-0.23 | 0.1-0.11 | 0.15-0.18 |
| Scaphocerite and antennular peduncle | exceeding it by about 0.25 its length | equal in length | exceeding it by about 0.2 its length | exceeding it by about 0.25 its length |
| Distal end of petasma: | | | | |
| ventromedian lobule | divided in two and fringed with fringed spinules | pincer-shaped end, no fringing spinules | pincer-shaped end, no fringing spinules | single rounded projection, with spinules |
| ventrolateral lobule | single rounded plate, with distal spinules | pair of plates of similar size, no spinules | pair of plates of dissimilar size, no spinules | single tapering plate with fringing spinules |
| Thelycal plate of 5th pereopods | a rounded projection, highest posteriorly | a sharp longitudinal ridge not extending over the 4th sternite | a large rounded longitudinal ridge extending well over the 4th sternite | a rounded projection with greatest height medially |

hepatic carina not extending beyond the posterior base of the branchiostegal spine. Branchiocardiac sulcus extending from near the posterior end of the hepatic sulcus to the level of the posterior margin of the carapace, the carina of similar length. Cervical sulcus reaching the dorsum, the carina much shorter than the sulcus. An ischial spine on the 1st pereopod. Thelycal plate of the 4th pereopods with a prominent transverse projection; that of the 5th pereopods with a rounded projection, widest anteriorly and round posteriorly, both projections glabrous.

REMARKS. This species is difficult to distinguish from *H. propinquus* (see discussion under this species; see also Table 1).

DISTRIBUTION. NW Australia, 450m. Known range, Japan, Philippines, Indonesia, NW Australia, Wallis and Futuna Is, 300-650m.

### **Hymenopenaeus halli** Bruce, 1966
(Fig. 8B)

*Hymenopenaeus halli* Bruce, 1966: 216, figs 1, 2; Crosnier, 1978, 1984, 1987, 1994a, b; de Freitas, 1985; Hayashi, 1985.

MATERIAL. QMW15858, 2M, 18.5, 20mm, 3F, 19.5, 20, 25mm; NTCR007957, 3M, 19, 20.5, 21mm; 008021,4M, 18.5,19, 19.5, 20mm, 4 F, 17.5, 20.5, 21, 23mm.

DIAGNOSIS. Carapace glabrous. Rostrum ascending and reaching from the middle to the end of the 2nd segment of the antennular peduncle; the ventral margin usually slightly concave; armed with 8 prominent teeth, including the epigastric. Adrostral carina prominent; postrostral carina becoming indistinct behind the cervical sulcus. Antennal, postantennal and hepatic spines prominent and of similar size; branchiostegal spine very prominent and raised well above the surface of the carapace. Hepatic carina ending at the posterior base of the branchiostegal spine; hepatic sulcus deep and extending posteriorly from just in front of the hepatic spine to its junction with the branchiocardiac sulcus, where it curves ventrally. Branchiocardiac sulcus deep and ending shortly before the posterior rim of the carapace; branchiocardiac carina blunt. A shallow orbitoantennal sulcus present. Cervical sulcus deep and reaching the dorsum, where it is interrupted by the postrostral carina; cervical and submarginal carinas sharp. Eye large, its maximum diameter 0.21-0.23 the length of the carapace. Prosartema not reaching as far as the eye. Antennular peduncle and scaphocerite of similar length. First pereopod with a basial and an ischial spine and a spine on the merus at about 2/3 its length. Ventro-median lobe of the petasma produced into a pincer-like projection; ventrolateral lobe with a pair of flattened, rounded apical plates, of similar size. Sternite of the female 4th pereopod with a very prominent, forwardly-directed spine;

the posterior margin with a pair of flat rounded plates; that of the 5th pereopod with a median carina extending for most of its length.

REMARKS. Bruce (1996) stated that there were two spines on the merus of the single type specimen. All the Australian specimens examined had only one spine, a feature also noted by Crosnier (1978). The pereopod on only one side of a specimen of *H. neptunus* in the present study was also double, so this appears to be an abnormality.

The four Australian *Hymenopenaeus* species are closely similar in appearance and may be difficult to distinguish from the key. Table 1 is an additional guide.

Colour in life is white-yellowish.

DISTRIBUTION. Off the east coast of Australia from 18°-33°47'S, depth range 500-1,000m. Known range, Madagascar to Indonesia, South China Sea, Philippines, Japan, E Australia, Wallis and Futuna Is, 450-1,000m.

**Hymenopenaeus neptunus**
(Bate, 1881)
(Fig. 8C)

*Haliporus neptunus* Bate, 1881; 1888; de Man, 1911.
*Hymenopenaeus neptunus* Crosnier & Forest, 1973; Crosnier, 1984, 1985, 1989, 1994a, b.

MATERIAL. QMW13511, M, 18.5mm, F, 20.5mm; 13525, 3F, 17, 19.5, 25.5mm; 13526, M, 15mm, 2F, 16, 18mm.

DIAGNOSIS. Rostrum variable, slightly to distinctly upcurved, slender, ventral margin convex and reaching from 2/3 to the tip of the 2nd segment of the antennular peduncle; with 6-7 teeth in all; adrostral carina prominent. Postrostral carina not interrupted by the cervical sulcus and extending a short distance behind it, where it becomes indistinct. Antennal, postorbital and hepatic spines large and of similar size; branchiostegal spine larger and very prominent. Only a faint indication of an orbito-antennal sulcus below the postorbital spine.

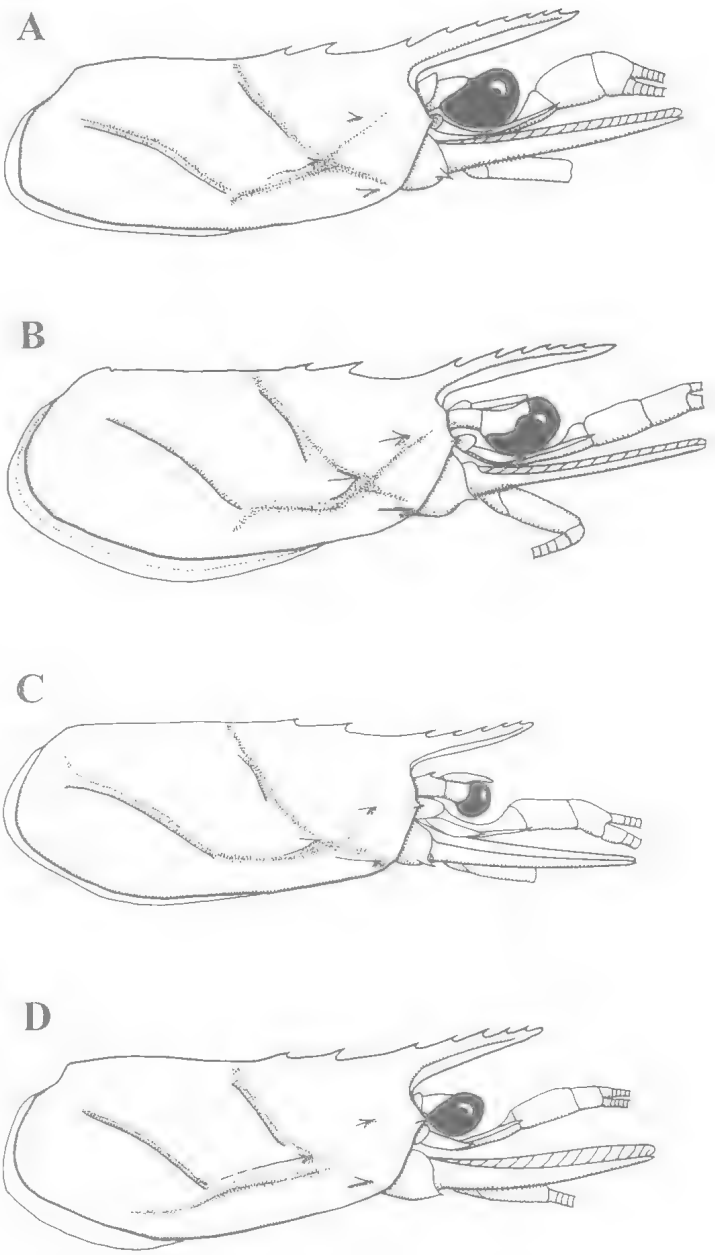



FIG. 8. A, *Hymenopenaeus aequalis* (Bate, 1888). NTCR000627, F, 13.7mm, 17°55'S 118°19'E, 450m. B, *Hymenopenaeus halli* Bruce, 1966. NTCR007957, M, 20.5mm, 19°S 150°39'E, 750m. C, *Hymenopenaeus neptunus* (Bate, 1881). QMW13511, M, 18.5mm, 18°10'S 148°32'E,1100m. D, *Hymenopenaeus propinquus* (de Man, 1907). NTCR007948, M, 13.5mm, 18°37S' 117°02'E, 506m.

Hepatic carina becoming rounded below the hepatic spine; hepatic sulcus wide and shallow above the branchiostegal spine, deepening below the hepatic spine and extending posteriorly to join the branchiocardiac sulcus. The latter deep, almost reaching the posterior dorsal margin of the carapace; branchiocardiac carina prominent, extending for about 0.75 the length of the sulcus. Cervical sulcus deep and meeting the postrostral carina without indenting it; cervical carina occupying the middle third of the sulcus. Eye small, maximum diameter of the cornea 0.1-0.11 the length of the carapace; prosartema about the same length as the eye. Scaphocerite exceeding the tip of the antennular peduncle by about 0.2 of its length. A large spine on the basis of the 1st pereopod and a spine on the merus at about 0.7 its length. Distal end of the ventromedian lobule of the petasma pincer-shaped, without fringing spinules; ventrolateral lobule with a distal pair of plates of dissimilar size. Thelycal plate of the 4th pereopods with a transverse ridge; that of the 5th pereopods with a prominent rounded longitudinal ridge which extends anteriorly as a pointed projection well over the posterior rim of the 4th sternite.

REMARKS. *H. neptunus* may be easily distinguished from the other Australian species of this genus by its very small eye. It is similar in this respect to *H. furici*, with which it is closely similar, as noted above. The thelyca could provide a satisfactory means of distinguishing the two species, as the thelycum of *N. neptunus* is very distinctive, but so far no females of *H. furici* have been described.

DISTRIBUTION. NE Australia, around 18°S 148°E, depth range1,000-1,200m. Known range, Indian Ocean to Indonesia, the Philippines, NE Australia, Wallis and Futuna Is, 700-1,500m.

**Hymenopenaeus propinquus** (de Man, 1907) (Fig. 8D)

*Haliporus propinquus* de Man, 1907: 140; de Man, 1911; de Man 1913.

*Hymenopenaeus propinquus* Burkenroad, 1936; Ramadan, 1938; Anderson & Lindner, 1943; Crosnier & Forest, 1973; Kensley, Tranter & Griffin, 1987; Crosnier, 1978, 1984a,b, 1985, 1989, 1994a, b; Burukovsky, 1974.

MATERIAL. NTCR007948, 3M, 13.5, 13.5, 14mm; 3F, 11.5, 14.2, 16mm; QMW15867, F, 19mm; 6F, 16.5, 20, 21, 21.5, 25.5, 26.5mm; 15871, 2M, 20, 22mm; 15873, 4F, 21, 21, 22.5, 23.5; 18056, M, 18.5mm; 3F, 22.5, 23, 24mm.

DIAGNOSIS. Rostrum acute, ascending, with 6-7 dorsal teeth, including the epigastric (rarely 8-10), and reaching from the middle to the end of the 2nd segment of the antennular peduncle; ventral margin almost straight; adrostral carina prominent; postrostral carina ending just before the cervical sulcus. Postorbital and hepatic spines prominent and of similar size; antennal spine smaller; branchiostegal spine very prominent, set back from the edge of the carapace, its tip well above the level of the carapace. Orbito-antennal sulcus barely discernable; hepatic carina extending posteriorly only to the base of the branchiostegal spine; hepatic sulcus deep, starting just anterior to the hepatic spine, usually ending well behind the beginning of the branchiocardiac sulcus and curving posterio-ventrally; branchiocardiac sulcus deep and ending level with the posterior rim of the carapace; anteriorly almost meeting the hepatic sulcus; branchiocardiac carina of similar length. Cervical sulcus deep and reaching the dorsum, the cervical carina well defined but markedly shorter than the sulcus. An ischial spine on the 1st pereopod, no spines on the basis or merus. Apex of the ventro-median lobe of the petasma rounded, edged with small spinules and with a minute incision; ventrolateral lobe with a single tapering apical plate. Thelycal plate between the 4th pereopods with a rounded median projection and covered uniformly with setae; plate between the 5th pereopods also a rounded projection, its greatest height across its middle region.

REMARKS. The rostrum of *H. propinquus* is usually sharper than that of *H. equalis*, but as noted previously is difficult to distinguish from it and also from *H. halli*. Table 1 compares the 4 Australian species.

Colour in life is white-yellowish.

DISTRIBUTION. NW Australia, east coast from 16°55'-33°43'S, 500-900m. Known range, Madagascar to Indonesia, Philippines, Australia, Wallis and Futuna Is, 450-1200m.

**Mesopenaeus** Pérez Farfante, 1977

*Mesopenaeus* Pérez Farfante, 1977: 331; Pérez Farfante & Kensley, 1997.

DIAGNOSIS. Body stout, carapace short and deep, integument thick, firm. Rostrum short, deep, ventral margin convex, no ventral teeth; epigastric and 1st rostral tooth separated by an interval similar to that between the 1st and 2nd teeth. Orbital, postorbital, antennal and hepatic spines present; branchiostegal and pterygostomian spines absent. Cervical sulcus almost

reaching the middorsum of the carapace; hepatic sulcus deep; branchiocardiac sulcus and carina, submarginal carina, lacking. Abdomen dorsally carinate from 3rd to 6th somites. Telson with a pair of prominent fixed subapical spines. Prosartema long and flexible. Antennular flagella not much longer than the carapace and dissimilar; dorsal flagellum subcylindrical and slender, ventral flagellum markedly depressed. Mandibular palp 2-segmented, the articles broad and of similar length. First pereopod with a fixed spine on the basis and ischium. Fourth and 5th pereopods not markedly slender proximally, 5th longer than the 3rd and 4th. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with a disto-lateral spine reaching the distal end of the lamella. Petasma simple, the distal part of the dorsolateral lobule projecting well beyond the apices of the adjacent lobules. Thelycum open, simple.

*Mesopenaeus* is similar to *Hadropenaeus*, but is distinguished from this and other solenocerids by its flattened ventral antennular flagella. *Mesopenaeus* is also similar in appearance to some *Solenocera* species, but these latter lack an external spine on the lateral ramus of the uropods, as well as possessing channelled ventral antennular flagella. All *Mesopenaeus* species inhabit a zone from the outer continental shelf to the upper half of the continental slope.

## KEY TO THE INDO-WEST PACIFIC SPECIES OF *MESOPENAEUS*

1. Rostrum usually with 7-8 dorsal teeth; scaphocerite about the same length as the antennular peduncle; ventral border of the merus of 1st pereopods with a large spine . . . . . *M. mariae*

Rostrum with 6 dorsal teeth; scaphocerite exceeding the antennular peduncle by about 0.2 its length; ventral border of the merus of 1st pereopods without a spine . . . . . *M. brucei*

Only three species of this genus have been described, the third, *M. tropicalis* (Bouvier, 1905) being from the Atlantic. *M. mariae* Pérez Farfante & Ivanov (1982) ranges from the Indian Ocean to Japan, but so far has not been collected from Australian waters. Thus *M. brucei* is the only Australian species.

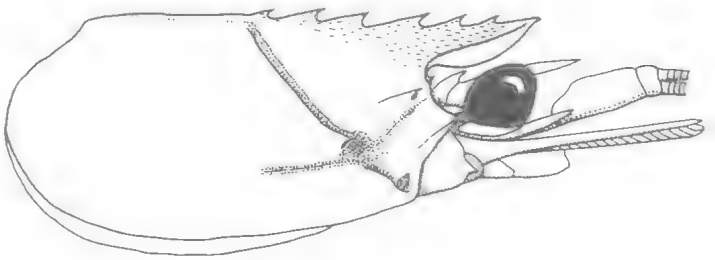


FIG. 9. *Mesopenaeus brucei* Crosnier, 1986. QMW15912, F, 26.5mm, 21°57'S 153°25'E, 330m.

**Mesopenaeus brucei** Crosnier, 1986
(Fig. 9)

*Mesopenaeus brucei* Crosnier, 1986: 20, figs 1,2; 1994b.

MATERIAL. QMW15912, F, 26.5mm; NTCR003028, 2M, 26.5, 27mm (paratypes); NTCR004564, F, 26mm (allotype).

DIAGNOSIS. Carapace glabrous, except on the rostrum and adjacent areas, and the pit in front of the hepatic spine where it is finely pubescent. Rostrum deep, reaching as far as the eye, with 6 very prominent teeth, including the epigastric, dorsal surface horizontal, the ventral margin strongly convex; postrostral carina well-defined behind the epigastric tooth, but gradually flattening towards the posterior margin of the carapace; tip of epigastric tooth at 0.52-0.55 the length of the carapace from its posterior margin. Orbital spine small, but distinct; antennal and hepatic spines large and of similar size, post-orbital spine larger. A shallow orbito-antennal sulcus present; hepatic sulcus sharp, but short, ending anteriorly in a shallow arc on the ventral side of a shallow, pear-shaped pterygostomian pit; hepatic sulcus deep, running from near the pterygostomian pit to the level of the 1st rostral tooth. Cervical sulcus deep, almost reaching the dorsum of the carapace, but not interrupting the postrostral carina; cervical carina sharp and almost the same length as the sulcus. Eye large; prosartema with a rigid spinous tip, devoid of setae and almost reaching half the 2nd antennular segment. Antennular flagella dissimilar, the dorsal flagellum subcylindrical, the ventral thicker and laterally compressed in its proximal part. First pereopod with basial and ischial spines; no spine on the merus. Ventromedian lobule of the petasma with a large distal shovel-shaped distal expansion.

REMARKS. The key features are the best for separating *M. brucei* from *M. mariae*. In addition the latter has a folded hat-like expansion of the ventromedial lobule of the petasma, whereas in *M. brucei* it is flat and shovel- or axe-shaped.

DISTRIBUTION. So far limited to Rowley Shoals, NW Australia (17°41'S 118°42'E); Arafura Sea (Indonesia, 9°49'S 130°07'E) and off Swain Reefs, NE Australia (22°35'S 153°48'E), 260-360m.

## **Solenocera** H. Lucas, 1849

*Solenocera* Lucas, 1849; Bate, 1881; Alcock, 1901; de Man, 1911; Stebbing, 1914; Burkenroad, 1934, 1936; Kubo 1949; Barnard, 1950; Balss, 1959; Pérez Farfante & Bullis, 1973; Crosnier, 1978; Pérez Farfante & Kensley, 1997.

*Parasolenocera* Wood-Mason & Alcock, 1891; Alcock, 1901.

DIAGNOSIS. Moderately robust, medium-sized prawns, with firm cuticle; pereopods well developed, pleopods not exceptionally long. Carapace glabrous except for the rostral area which is setose. Antennular flagella wide and when apposed forming a respiratory tube, often as long or longer than the carapace. Rostrum laterally compressed, usually deep and not exceeding the 1st segment of the antennular peduncle and with dorsal teeth only. Postorbital, antennal and hepatic spines present; branchiostegal and pterygostomian spines present or absent, but never with both. Cervical sulcus reaching to or almost to the dorsal midline. First and 2nd abdominal somites narrowing towards the dorsal mid-line so that the cephalothorax may be flexed almost at right angles to the abdomen. Exopods on thoracic somites 1 to 7. Telson usually armed with fixed subapical spines, never with lateral moveable spines. Lateral ramus of uropod without a distolateral spine.

The species of this genus are inhabitants of the continental shelf and slope, from about 15m down to several hundred metres, sometimes to greater depths. The body form suggests that they are predominantly benthic and environmental data for a few species indicate that soft substrates are preferred. The long respiratory tube and ability to flex the cephalothorax upwards almost 90° to the abdomen, indicates that they bury deeply in these soft sediments. It is by far the largest genus within the Solenoceridae, with at least 21 Indo-West Pacific species, mostly with similar facies.

### KEY TO THE INDO WEST PACIFIC SPECIES OF *SOLENOCERA*

1. Pterygostomian spine present . . . . . 2
   Pterygostomian spine absent . . . . . 4
2. Postrostral carina distinct behind the cervical sulcus; anterior part of the hepatic carina recurved posteriorly to form a quadrangular lobe . . . . . 3
   Postrostral carina absent behind the cervical sulcus; anterior part of the hepatic carina almost straight . . . . . *S. comata*
3. Cervical carina with a shallow notch about 1/3 its length above the hepatic spine . . . . . *S. africana*
   Cervical carina without a notch . . . . . *S. algoensis*
4. Postrostral carina reaching to, or almost to, the posterior border of the carapace and clearly defined along its length . . . . . 5
   Postrostral carina extending little if any beyond the cervical sulcus, or poorly defined . . . . . 13
5. Postrostral carina interrupted by a deep notch at the level of the cervical sulcus . . . . . 6
   Postrostral carina not interrupted by a deep notch at the level of the cervical sulcus (often a shallow depression in this region). . . . . 8
6. Postrostral carina high and blade like; postrostral sulcus feebly developed, less than 1/3 the length of the carina or absent. . . . . 7
   Postrostral carina low along its length; postrostral sulcus more than 1/2 the length of the carina and widening posteriorly . . . . . *S. koelbeli**
7. Postrostral carina highest posteriorly, sloping steeply towards the posterior border of the carapace . . . . . *S. alticarinata*
   Postrostral carina highest anteriorly, tapering gradually towards the posterior border of the carapace . *S. choprai*
8. Telson without a pair of subapical fixed spines . . . . . *S. crassicornis***
   Telson with a pair of subapical fixed spines . . . . . 9
9. Post-rostral carina behind the cervical sulcus distinctly humped in profile, with a median tooth or with a small median nodule†; branchiocardiac sulcus and carina well defined, the former running from the posterior edge of the carapace almost to the hepatic sulcus . . *S. alfonso*†
   Post-rostral carina behind the cervical sulcus only slightly and smoothly convex in profile and without a median tooth or nodule; branchiocardiac sulcus and carina feebly defined . . . . . 10
10. Anterior part of the hepatic carina slightly curved, but not bordering the ventral side of a clearly-defined shallow depression at its anterior end . . . . . *S. bifurcata*
    Anterior part of the hepatic carina distinctly curved and bordering the ventral side of a clearly-defined shallow depression at its anterior end. . . . . 11
11. Anterior part of the hepatic carina forming a shallow arc, much less than a semicircle, round the lower border of a shallow depression near the pterygostomian angle; ventral margin of rostrum convex . . . . . 12
    Anterior part of the hepatic carina forming a deep, upward-facing arc, almost a semicircle, round the lower border of a shallow depression near the pterygostomian angle; ventral distal margin of rostrum usually straight, sometimes slightly concave . . . . . *S. melantho*

12. Postrostral sulcus a series of pits and not dividing the carina into two posteriorly; north Australian seas . . . . . *S. australiana*

Postrostral sulcus consisting of long depressions and pits, usually dividing the carina into two posteriorly; Malaysia, Strait of Malacca. . . . . *S. halli*

13. Anterior end of hepatic carina curving ventroposteriorly, blunt or forming a sharp, almost spinous point. . . . 14

Anterior end of hepatic carina not curving posteriorly, either straight or ending in an upward-facing arc . . 20

14. Anterior hepatic carina sharp or spinous . . . . . 15

Anterior hepatic carina blunt or forming an angle. . . 18

15. Rostrum short, reaching about half the length of the cornea . . . . . 16

Rostrum reaching or exceeding the distal end of the cornea . . . . . *S. barunajaya*

16. Dorsal carina present on abdominal somite 3; maximum diameter of the eye equal to or exceeding 0.18 the length of the carapace; prosartema not reaching as far as the eye . . . . . 17

Dorsal carina absent on abdominal somite 3; eye small, maximum diameter about 0.14 the length of the carapace; prosartema exceeding the distal end of the cornea. . . . . *S. faxoni*

17. Usually 7 rostral spines, including the epigastric; hepatic carina ending in a spine that just reaches the anterior border of the carapace; no spine on the basis of the 2nd pereopod . . . . . *S. spinajugo*

Usually 6 rostral spines, including the epigastric; hepatic carina ending in a prominent point that exceeds the antero-ventral border of the carapace; a spine on the basis of the 2nd pereopod . . . . . *S. moosai*

18. Rostrum short, not reaching as far as the distal end of the eye; anterior end of hepatic carina rounded . . . . . 19

Rostrum long, well exceeding the eye, and reaching to about half the 2nd segment of the antennular peduncle; anterior end of hepatic carina almost angular . . . . . *S. annectens*

19. Six or seven rostral teeth including the epigastric; inferior antennular flagellum with 39-53 segments *S. pectinulata*

Eight or nine rostral teeth including the epigastric; inferior antennular flagellum with 57-77 segments . . . . . *S. pectinata*

20. Rostrum slender, reaching about 1/3 the length of the cornea . . . . . *S. bedokensis* ††

Rostrum deep, reaching at least 1/2 the length of the cornea . . . . . 21

21. Epigastric tooth well behind the level of the hepatic tooth; ventral margin of rostrum strongly convex; length of the superior antennular flagellum 1.3-1.43 times that of the carapace and the inferior flagellum with 55-59 segments . . . . . *S. rathbuni* §

Epigastric tooth at about the level of the hepatic tooth; ventral margin of rostrum slightly convex; length of the superior antennular flagellum 2.1-2.2 times that of the carapace; inferior flagellum with 89-109 segments . . . . . *S. waltairensis* §§

* *S. koelbeli* Starobogatov, 1972 is probably a synonym of *S. alfonso* form *inermis* (Ivanov, 1994).

** =*S. subnuda* Kubo, 1949; see discussion under *S. bifurcata*.

† See discussion under *S. alfonso*.

†† *S. bedokensis* Hall was described from one damaged specimen and may not be a valid species; it is similar to *S. utinomii* Kubo (also described from one damaged female). Also *S. zarenkovi* Starobogotov is so badly damaged that its identity must remain very doubtful (Ivanov, 1994).

§ *S. phuongi* Starobogotov is probably a junior homonym of this species (Ivanov, 1994).

§§ The identity of *S. gurjanovae* Starobogotov is doubtful; it may be conspecific with *S. waltairensis* (Ivanov, 1994).

*S. hexti* Alcock has not been included, because Alcock (1901: 20) considers that the antennules could not form a respiratory tube, suggesting a *Mesopenaeus* species; also the flagella are shorter than the carapace, another *Mesopenaeus* feature. The figure in Starobogatov (1972) clearly shows a suprahepatic spine, which indicates a *Gordonella* or *Haliporoides* species, but the carapace shape is that of a *Solenocera* or *Mesopenaeus*.

The following 14 species have been identified from Australian waters : *S. alfonso*, *S. annectans*, *S. australiana*, *S. barunajaya*, *S. choprai*, *S. comata*, *S. bifurcata* sp. n., *S. faxoni*, *S. koelbeli*, *S. melantho*, *S. moosai*, *S. pectinata*, *S. pectinulata*, *S. rathbuni*.

### **Solenocera alfonso** Pérez Farfante, 1981 (Fig. 10)

*Solenocera alfonso* Pérez Farfante, 1981: 631, figs 1-5.
*Solenocera alfonso*, form *alfonso* and form *inermis* Crosnier, 1989: 58.

MATERIAL. Form *alfonso*: NTCR006632, F, 30mm; NTCR007924, 2F, 30, 31.5mm. Form *inermis*: QMW15799, F, 16.5mm.

DIAGNOSIS. Rostrum deep, almost straight dorsally, convex and upturned ventrally, with 6-8, usually 7 teeth. Form *alfonso*: Postrostral carina distinctly convex, but low and broad, well-defined anteriorly and with a spine about midway between the top of the cervical sulcus and the posterior border of the carapace; carina tapering to zero behind the tooth; postrostral sulcus represented by a series of pits behind the tooth, sometimes anterior to it as well. Form *inermis*: Similar to form *alfonso*, but with only a small nodule in place of the median tooth. Both forms: A small orbital spine present; antennal and hepatic spines of similar size, the postorbital spine larger. Cervical sulcus deep, not quite reaching the dorsum, which is slightly depressed at this point. Hepatic carina beginning just anterior to the hepatic spine and forming a sharp edge bordering a pterygostomian pit. Hepatic sulcus posteriorly not quite reaching the level of the top of the cervical sulcus, where it curves ventrally. Branchiocardiac sulcus well defined,

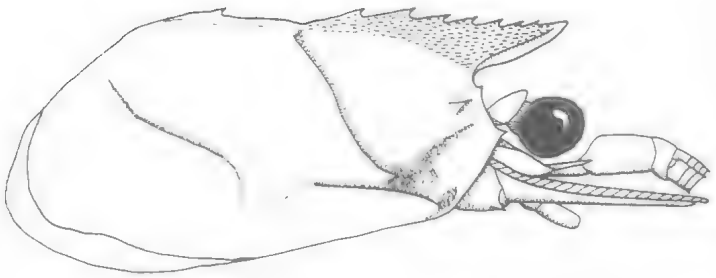


FIG. 10. *Solenocera alfonso* Pérez Farfante, 1981. NTCR007924, F, 30mm, 9°40'S 129°54'E, 298m.

extending from near the posterior margin of the carapace to a broad downward arc, almost meeting the hepatic sulcus; branchiocardiac carina present, but only equal to about 1/2 the length of the sulcus. Thelycum almost featureless; this and other characteristics of the genitalia as described by Pérez Farfante (1981).

REMARKS. As pointed by Pérez Farfante (1981) this large species is distinctive, the spine on the postrostral carina being the most obvious single feature. However Crosnier (1989) has identified a form without a spine, being identical in other respects, and naming it form *inermis*, the type being form *alfonso*. Crosnier notes that the 2 forms of *S. alfonso* were never collected from the same locality in the Philippines, but the presence of form *inermis* off NE Australia indicates that this form is not limited to the Philippines. Form *inermis* could be confused with *S. australiana*, *S. halli* and *S. melantho* and the key includes distinctive features of *S. alfonso* besides the postrostral spine. Crosnier (1989) gives a detailed analysis of the differences separating these four species.

DISTRIBUTION. Australian waters in the Arafura Sea, 283-298m. Known range, Philippines, N Australia, 90-550m.

**Solenocera annectens** (Wood-Mason, 1891)
(Fig. 11)

*Parasolenocera annectens* Wood-Mason in Wood-Mason & Alcock, 1891: 276; Alcock & McArdle, 1901; Alcock, 1901.
*Solenocera annectens* Crosnier, 1984, 1989, 1994.

MATERIAL. NTCR007077, F, 23.5mm.

DIAGNOSIS. Rostrum straight and tapering, reaching about half the 2nd segment of the antennular peduncle; with 7-8 teeth close together and widely separated from the epigastric, which is at 1/3 the carapace. Postrostral carina ending at the top of the cervical sulcus, the dorsum being slightly indented at this point. A small orbital spine present; antennal and hepatic spines of similar size, postorbital spine larger. Orbito-antennal sulcus short, reaching about the level of the antennal spine. Hepatic carina short and starting in front of the tip of the hepatic spine and forming a blunt point at its anterior end, which projects beyond the pterygostomian angle. Hepatic sulcus posteriorly reaching the level of the top of the cervical sulcus, where it curves downward. Branchiocardiac sulcus deep, reaching almost to the posterior border of the carapace and curving ventrally at its anterior end, not quite meeting the hepatic sulcus. Genitalia as described by Crosnier (1984).

REMARKS. The long, tapering rostrum of this species is distinctive. It appears to be a deeper water solenocerid.

DISTRIBUTION. NW Australia 14°01'S 122°08'E, 443m. Known range, Andaman Sea, Indonesia, Philippines, Arafura Sea, nearly always at depths greater than 400m down to 900m.

**Solenocera australiana**
Pérez Farfante & Grey, 1980
(Fig. 12, 19B)

*Solenocera australiana* Pérez Farfante & Grey, 1980: 421-434, figs 1-5; Grey et al., 1983; Crosnier, 1989.

MATERIAL. QMW12826, F, 28mm; 15838, F, 32.5mm; 17417, 2F, 20, 22mm; 17419, F, 33.5mm; 18084, F, 37.5mm; 18085, M, 21.5mm, 2F, 27.5, 31mm.

DIAGNOSIS. Rostrum deep and reaching to about the extremity of the eye; with a total of 8-10 teeth, usually 9, with the 4th or 5th above the orbital margin. Postrostral carina well defined, blunt and reaching almost to the posterior edge of the carapace; postrostral sulcus usually a series of pits, sometimes formed into a short sulcus, usually with pits. Orbital angle sharp, antennal and hepatic spines of similar size, postorbital spine large; cervical sulcus reaching almost to the dorsum, which is only barely indented at this point. Orbito-antennal sulcus deep, almost vertical and reaching the base of the postorbital spine. Anterior hepatic carina curving ventrally round an ovoid shallow depression at the pterygostomian angle, forming an arc much less

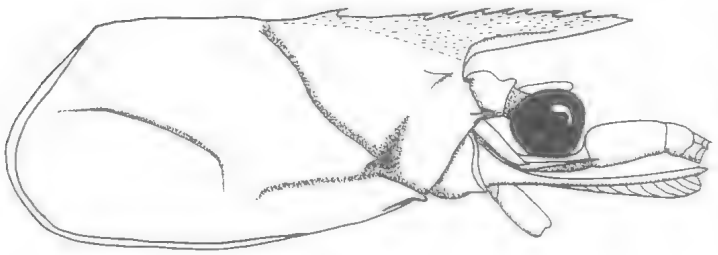


FIG. 11. *Solenocera annectans* (Wood-Mason, 1891). NTCR007077, F, 23.5mm, 14°01'S 122°08'E, 443m.

than a semicircle (Fig.19B). Hepatic sulcus extending posteriorly and almost joining the branchiostegal sulcus, which is indistinct, but almost reaches the posterior edge of the carapace. Antennular flagella 1.4-1.7 the length of the carapace, longer in juveniles. Coxa of the 5th pereopod in mature females bearing a large, forwardly-directed spine, which reaches almost as far a the anterior edge of the segment. For details of petasma and thelycum see Pérez Farfante & Grey (1980, figs 4, 5).

REMARKS. *Solenocera australiana* has been confused with *S. melantho*, which also occurs in Australian seas. Features distinguishing these two species are listed under the latter species. *S. halli* (not recorded from Australia) also has close affinities with these two and all three are compared in detail in Pérez Farfante & Grey (1980). See also comments under *S. alfonso*.

Carapace colour in life, pink red to orange; telson, pleopods, uropods, dark red; antennular flagella, bright red (see colour photograph in Grey et al., 1983, pl. 5).

DISTRIBUTION. So far known only from Australian seas, from NW Australia to NE Queensland, 15-70m.

**Solenocera barunajaya** Crosnier, 1994
(Fig. 13)

*Solenocera barunajaya* Crosnier, 1994a: 355-9, figs 1a-c, 2a, 3a-e.

MATERIAL. NTCR000621: M, 13.5mm, 2F, 22.5mm each; 012296: F, 29mm; 012297: 2F, 23, 25mm; 012298: 4F, 27.5, 28, 28mm, 1 damaged.

DIAGNOSIS. Rostrum slightly upcurved and sharply pointed, usually with six teeth including the epigastric and reaching as far as, or slightly exceeding the distal extremity of the cornea. Only the blade of the rostrum above the adrostral carina is finely setose, the carapace entirely glabrous. Postrostral carina reaching only to the posterior edge of the cervical sulcus. Orbital angle blunt, antennal and hepatic spines small, postorbital spine large. Hepatic carina forming a prominent, sharply angular point anteriorly, raised well above the level of the carapace and projecting beyond its margin; underneath this projection, a short channel runs parallel to and just inside the pterygostomian rim of the carapace. Posteriorly, the hepatic carina reaches to the base of the hepatic spine. Hepatic spine overlying a deep pit, with a well-defined posterior orbito-antennal sulcus running towards the base of the post-orbital spine, where it becomes confluent with the shallower anterior part. Cervical sulcus reaching the dorsum, the carina ending a little below this and interrupted at its mid-point by a shallow sulcus, which extends postero-ventrally, reaching the branchiostegite, and forming a junction with the posterior end of the hepatic sulcus and the branchiocardiac sulcus. The latter well-defined and reaching almost to the level of the posterior dorsum of the carapace; branchiocardiac carina not defined. Thelycum with two large and two small anterior bosses, posteriorly with two large, but low bosses, separated by a median longitudinal sulcus (for full descriptions and figures of thelycum and petasma see Crosnier, 1994a).

REMARKS. *S. barunajaya* is similar in appearance to *S. faxoni*, but the small eye of the latter is distinctive. *S. spinajugo* and *S. moosai* are also similar, but the key characters should enable them to be readily separated.

DISTRIBUTION. So far known only from NW Australia, 9°45'-18°19'S, 118°9'-130°E, the Kai

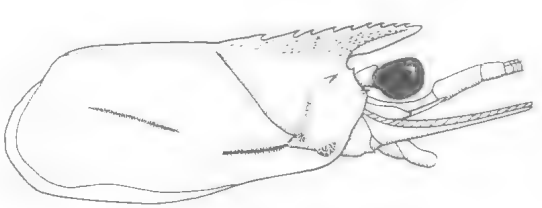


FIG. 12. *Solenocera australiana* Pérez Farfante & Grey, 1980. QMW17419, F, 33mm, Gulf of Carpentaria, 53mm.

and Tanibar Is in the Arafura Sea (the type locality), 240-370m.

**Solenocera bifurcata** sp. nov
(Fig. 14A-F)

MATERIAL. HOLOTYPE. QMW2385, F, 24mm, off Cape Moreton, SE Qld, depth approx. 200m. ALLOTYPE: QMW18029, M, 19mm, 17°53'S 146°53'E, (off Mission Beach, NE Qld) 162-170m. PARATYPE: QMW4680, F, 26.5mm, off Cape Moreton, SE Qld, depth approx. 200m.

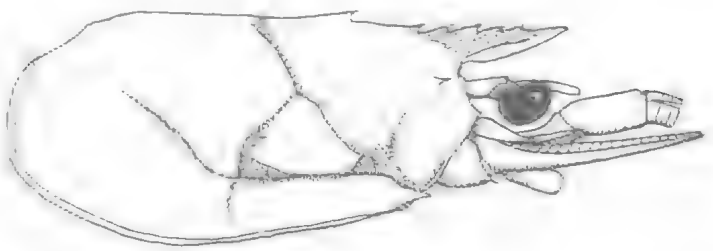


FIG. 13. *Solenocera barunajaya* Crosnier, 1994. NTCR012298, F, 28mm, 9°46'S 129°54'E, 298m.

DESCRIPTION. *Rostrum, carapace, abdomen* (Fig. 14A). Rostrum slightly downcurved with strongly convex lower margin, reaching about half the length of the cornea; with 6-7 teeth including the epigastric; adrostral carina ending at about the level of the last (sub-apical) rostral tooth. Postrostral carina low, almost reaching the posterior margin of the carapace and slightly indented at the level of the cervical sulcus. Carapace entirely glabrous, a setose area confined to the rostrum. Orbital angle blunt, postorbital and hepatic spines large, antennal spine small. Hepatic carina almost straight anteriorly and bordering a shallow depression just inside the pterygostomian angle; posterior end reaching the base of the antennal spine. Posterior end of the hepatic sulcus reaching about the level of the top of the cervical sulcus. Branchiocardiac sulcus barely distinguishable and occupying approximately the middle third of the branchial region. Cervical sulcus deep and not quite reaching the postrostral carina. Dorsal carina of the abdomen beginning at about the anterior third of the 2nd abdominal somite and well developed on the 3rd to 6th somites. Telson with a pair of subapical fixed spines at about 0.16 its length from the tip.

*Appendages.* Maximum diameter of the cornea about 0.2 the length of the carapace; prosartema reaching as far as the eye; stylocerite reaching about 0.7 the length of the cornea. Antennular flagella 0.7-0.9 the length of the carapace, the ventral flagellum with 46-50 segments, the tip tapering abruptly (Fig.14F). Scaphocerite barely exceeding the antennular peduncle, the tip of the blade slightly exceeding the disto-lateral spine; antennal flagellum about 5 times the length of the carapace. Third maxilliped exceeding the antennular peduncle by at least part of the propodus; the 1st pereopod reaching as far as the eye; the 2nd reaching the tip of the antennular peduncle; the 3rd exceeding the tip of the antennular peduncle by at least the propodus; the 4th exceeding the peduncle by the propodus; the 5th incomplete in all specimens, but with the tip of the merus reaching as far as the eye.

*Petasma and Appendix Masculina.* Apex of ventromedian lobe of the petasma flat and fringed with spinules, aligned medially; apex of dorsolateral lobe with long spinules and a ventral projection that partly encloses the ventrolateral lobe distally; the latter with two small teeth near the recurved tip (Fig. 14B). Accessory lobule present with about 16 spinules (Fig. 14C). Outer basal projection of appendix masculina rounded and small; inner and outer appendices elongate, subequal in length and tipped with short spinules (Fig. 14E).

*Thelycum* (Fig. 14D). Coxae of the 4th pereopods with medial tooth-like projections, which almost meet on the midline; behind these a pair of postero-lateral projections on the posterior rim of the sternite. Coxae of the 5th pereopods with a pair of prominent spines, directed antero-ventrally; behind these a pair of large flat medially-directed plates. Just in advance of these plates a single median prominent ovoid conical projection arising from the sternum, with an apical transverse bifurcate projection (more prominent in the paratype than in the holotype).

REMARKS. *S. bifurcata* is superficially similar to *S. subnuda* Kubo (1949) and Hall (1962), but differs substantially in a number of features. However, *S. subnuda* has been relegated to the status of a synonym of *S. crassicornis* Milne Edwards, (H. Milne Edwards, 1837) by Starobogatov (1972) and Liu & Zhong (1986), probably because both species have unarmed telsons, a unique feature in the Solenoceridae. There is little doubt that the species described by these four authors are identical, but the identity of *S. crassicornis* is confused. Bate (1881), who had access to the type from Bombay, noted that it agreed with the author's description. He also had

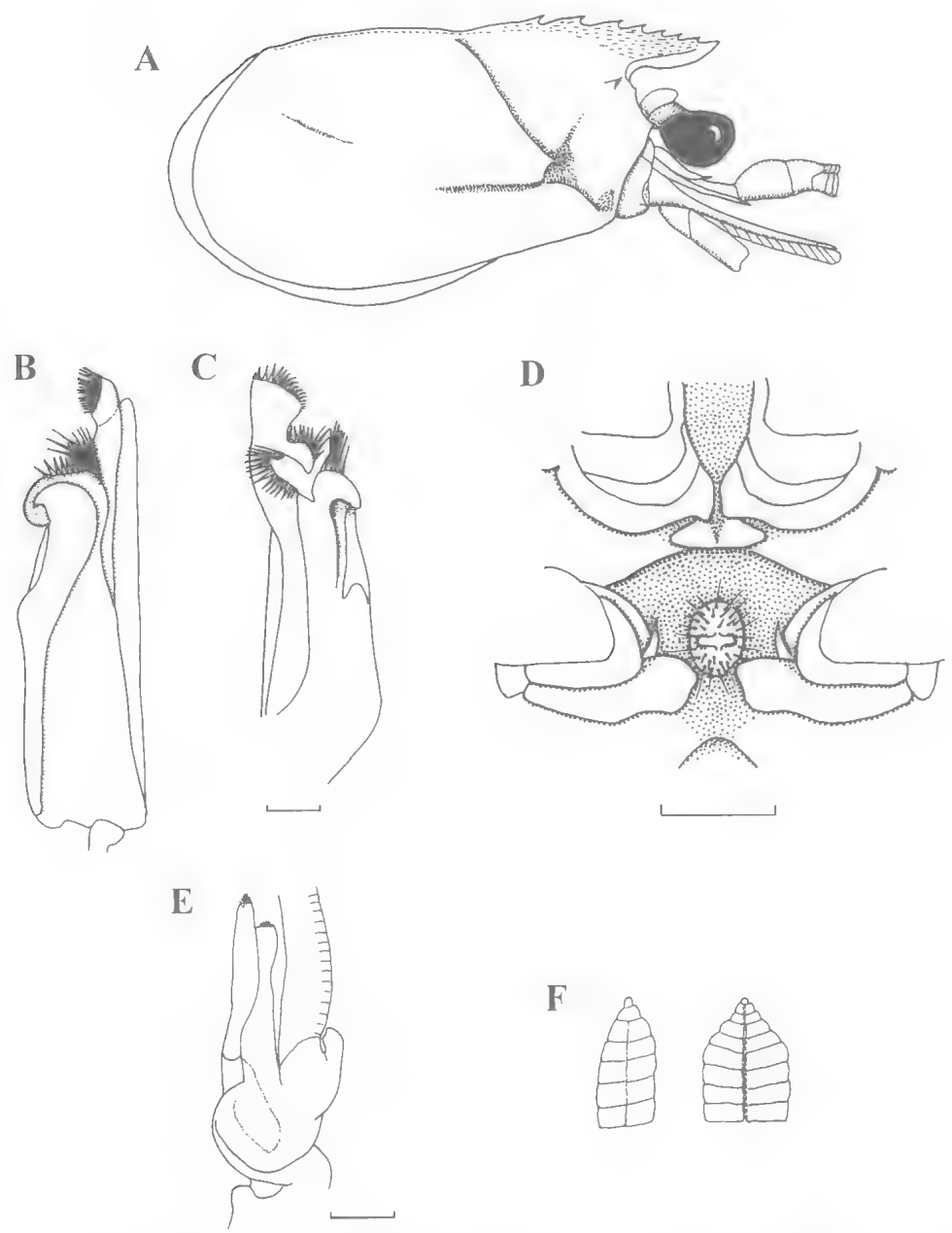



FIG. 14. A, *Solenocera bifurcata* sp. nov. QMW2385, holotype, F, 24mm, southeast Queensland, approx. 200m; B, right half of petasma of allotype, ventral aspect (scalebar = 1mm); C right half of petasma, external aspect; D, thelycum, holotype (scalebar = 1mm); E, Appendix masculina, allotype (scalebar = 1mm); F, tips of upper and lower antennular flagella, holotype.

'Challenger' collection material from 'between Borneo and the Philippine Islands'. Since *S. subnuda* has been described from this area, it could be regarded as further evidence that it is a synonym of *S. crassicornis*. Wood-Mason & Alcock (1891) refer to 'the common Indian littoral form (?*P. crassicornis*)', which lacked a branchiostegal spine, but Bouvier (1908) stated that *S. crassicornis* had 10-12 rostral teeth and a branchiostegal spine. However, no *Solenocera* species have 10-12 rostral teeth and it seems likely that Bouvier had confused it with a species

of another genus. Then Kubo (1949) used Bouvier's (1908) description to separate his species, *S. subnuda* from *S. crassicornis*. Examination of the type would resolve the problem, but Burkenroad (1934) noted that the type no longer existed. Dr A. Crosnier (pers. comm.) considers that *S. subnuda* is an undoubted synonym of *S. crassicornis*. Table 2 lists the differences between *S. bifurcata* and the published descriptions of *S. subnuda* (=*S. crassicornis* ).

DISTRIBUTION. Unfortunately, the depths of collection of both the holotype and paratype are not known exactly, but were probably between 100-200m. The allotype was collected from between 162-170m.

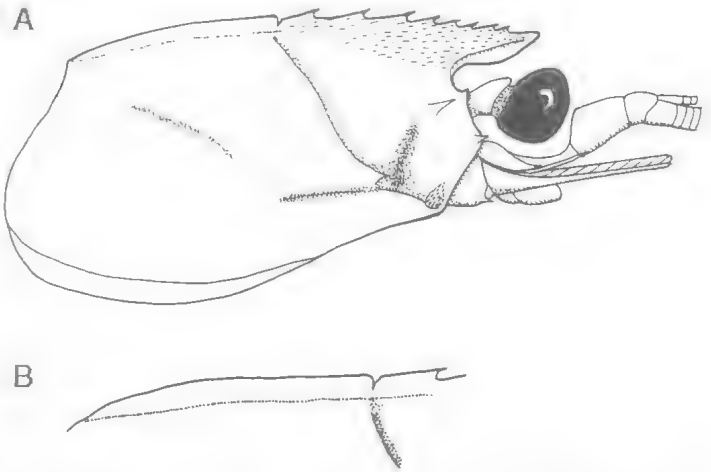



FIG. 15. A, *Solenocera choprai* Nataraj, 1945. QMW18025, F, 28mm, 17°53'S 146°54'E, 162-170m; B, postrostral carina, QMW18026, M, 29mm, 18°07'S 147°11'E, 200m.

**Solenocera choprai** Nataraj, 1945
(Fig. 15A, B)

*Solenocera choprai* Nataraj, 1945: 91, figs 1-4; George, 1969; Starobogatov, 1972; Tirmizi, 1972, Crosnier, 1978, 1984, 1989, 1994; Grey et al., 1983 (Non pl. 4 = *S. alticarinata*); de Freitas, 1985; Kensley, Tranter & Griffin, 1987.

*Solenocera alticarinata* Hall, 1961, 1962; Starobogatov, 1972, pl. 2, fig. 5a-b.

*Solenocera koelbeli* Burkenroad, 1959.

MATERIAL. QMW15827, M, 21mm, F, 24mm; 15861, 2M, 23.5, 25mm; 15870, 6M, 22-26mm; 15919, F, 22.5mm; 15921, 2F, 26.5, 28mm; 18025, 4F, 25-32.5mm; 18026: 2M, 24, 29mm, 2F, 28, 32.5mm.

DIAGNOSIS. Rostrum slightly downcurved, ventral edge strongly convex, reaching about 0.75 of the eye, with 7-8 dorsal teeth in all, exceptionally 9. Cervical sulcus deep and almost reaching the mid-dorsum, a deep narrow cleft immediately above its end. Postrostral carina high and narrow, its anterior end about the same height as the epigastric tooth, usually decreasing in height throughout its length and ending at the posterior edge of the carapace; sometimes of uniform height, or even slightly rising, through most of its length; a short postrostral sulcus or series of pits present. Hepatic carina ending at the edge of a small round pit just behind the pterygostomian angle. Orbital angle sharp; a small postorbital pit above the postorbital spine; branchiocardiac carina and sulcus well defined. Antennular flagella 1.15-1.4 (mean 1.25) the length of the carapace. Fifth pereopod long and slender and exceeding the tip of the antennular peduncle by 0.5-0.75 the length of the propodus. Petasma and thelycum as figured by Crosnier (1978).

REMARKS. *S. choprai* closely resembles *S. alticarinata* Kubo. The latter could be considered a synonym or perhaps a subspecies, but Crosnier (1978, 1989), who examined a number of specimens of both species, found the differences separating them to be consistent, while admitting these were small. In *S. alticarinata* the postrostral carina increases in height towards the posterior end, whereas in *S. choprai* it usually decreases. However, in some Australian specimens it maintains the same height for about 3/4 of its length, or actually increases slightly (Fig. 15B). Crosnier (1978) also found differences in the thelycum, but so far the petasma of *S. alticarinata* has not been described and figured. *S. alticarinata* appears to be limited to E Asian seas, from the Philippines to Japan, but *S. choprai*, although overlapping in the Philippines, ranges from the Indian Ocean to E Australia.

DISTRIBUTION. From NE Australia from 17°57' to 28°S and NW Australia, 100-200m. Known range, Madagascar to the Gulfs of Suez and Arabia, Pakistan, India, Malaysia, Philippines, through Indonesia to the Kai and Tanimbar Is in the Arafura Sea to E Australia, 50-200m.

TABLE 2. Principal differences between *S. bifurcata* and *S. subnuda* (=*S. crassicornis* ) .

| Character | *S. bifurcata* | *S. subnuda* |
|---|---|---|
| Rostral teeth | 6-7 | 8-10 |
| Branchiocardiac sulcus | feeble & short | deep & long |
| Armature of adult telson | 2 sub-apical fixed spines | no sub-apical or other spines |
| Dorsomedian lobule of petasma | not projecting distally | projecting distally and slightly recurved ventrally |
| Apex of ventrolateral lobule of petasma | recurved apically with two teeth, partly enclosed by base of dorsolateral lobule | apex directed laterally, not recurved and not partly enclosed |
| Thelycum | coxa of 5th pereopod with large inner plate and a spine | coxa of 5th pereopod without inner plate or spine |
| Median boss of thelycum | apex bifurcate | apex not bifurcate |

## **Solenocera comata** Stebbing, 1915 (Fig. 16)

*Solenocera comatum* Stebbing, 1915: 67, pls 13-14; Barnard, 1950; Kensley, 1972, 1974.
*Solenocera comatus* Burkenroad, 1934, 1939; Anderson & Lindner, 1945.
*Solenocera brevipes* Kubo, 1949.
*Solenocera comata* Starobogatov, 1972; Crosnier, 1978, 1984, 1985, 1994; Hayashi, 1984a.

MATERIAL. NTCR007950, M, 12.5mm; 5F, 13, 13.5, 16, 17, 18mm.

DIAGNOSIS. The setose area around the rostrum, typical of the genus, extends further laterally than in other species, but is sparse. Rostrum small and short, reaching about half the cornea; strongly convex ventrally with tip down-turned horizontally; with 5 rostral teeth in all, the epigastric separated from the other teeth which are close together and evenly spaced. Postrostral carina ending at the level of the top of the cervical sulcus. Orbital angle blunt; postorbital, antennal and hepatic spines large; pterygostomian spine present. Posterior orbito-antennal sulcus short and shallow. Hepatic carina starting just in front of the hepatic spine and ending at the the edge of a shallow, sparsely setose, pterygostomian depression. Hepatic sulcus ending posteriorly to a level with the top of the cervical sulcus. Cervical sulcus reaching the dorsum, which is barely depressed at this point; only faint indications of a branchiocardiac sulcus. Petasma and thelycum as described by Crosnier (1978).

REMARKS. This is one of the two species of *Solenocera* so far recorded which have a pterygostomian spine. The other is *S. algoensis*, which has a recurved hepatic carina and which has been recorded only in the western Indian Ocean.

DISTRIBUTION. NW coast of Australia, 15°58'S 120°45'E, 297m. Known range, Western Indian Ocean, Indonesia, Timor Sea, Philippines, Japan, 90-460m.

## **Solenocera faxoni** de Man, 1907 (Fig. 17)

*Solenocera faxoni* De Man, 1907: 136; 1911: 52, 1913, pl. 5; Kubo, 1949; Crosnier, 1984; Hayashi, 1984a; Kensley, Tranter & Griffin, 1987.

MATERIAL. QMW11421, F, 23.5mm; 13505, F, 27mm; 15308, F, 20mm.

DIAGNOSIS. Rostrum deep proximally, sharply pointed towards the tip, with 5-7 rostral teeth, including the epigastric. Postrostral carina ending opposite the top of the cervical sulcus. Orbital angle weak; postorbital and hepatic spines large, antennal spine small; posterior orbito-antennal sulcus wide but well defined. Hepatic carina ending anteriorly in a sharp point, elevated above the level of the carapace, and ending posteriorly level with the base of the hepatic tooth; hepatic sulcus deep posteriorly and meeting a well-defined transverse sulcus, which runs from the lower branchiostegite to the cervical carina, defining a triangular hepatic area; branchiocardiac sulcus not defined. No dorsal carina on the 3rd abdominal somite. Maximum diameter of the cornea about 0.14 the length of the carapace. Antennular flagella about 1.1 the length of the carapace in the 20 and 27mm specimens above, and 1.3 in a 11.8mm specimen (Crosnier, 1984). Distal edge of the dorsomedian

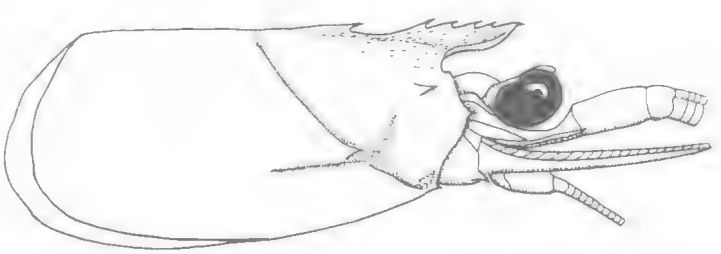


FIG. 16. *Solenocera comata* Stebbing, 1915. NTCR007950, F, 18mm, 15°58'S 120°45'E, 297m.



FIG. 17. *Solenocera faxoni* de Man, 1907. QMW15308, F, 20mm, 28°04'S 153°57'E, 400m.

lobe of the petasma entire, thelycal plate between the 5th pereopods with a median sulcus and no anterior boss.

*Solenocera faxoni* is similar to *S. moosai* and the main features separating the two species are discussed under the latter.

DISTRIBUTION. Australian seas from 33°27' to 17°57'S; Timor Sea and off NW Australia, off Marmion, near Perth (32°S), 380-400m. Known range, Kai I., Indonesia, around N Australia and to Japan, 200-400m; appears to be an uncommon species.

**Solenocera koelbeli** de Man, 1911
(Fig. 18A, B )

*Solenocera koelbeli* de Man, 1911: 48; Crosnier, 1978, 1985, 1989; non Starobogatov, 1972.
*Solenocera distincta* Koelbel, 1884; Yokoya, 1933.
*Solenocera depressa* Kubo, 1949.
*Solenocera vietnamensis* Starobogatov, 1972.
*Solenocera melantho* Lee & Yu, 1977.

MATERIAL. WAMC25273, M, 20mm; 25274 F, 31mm.

DIAGNOSIS. Blade of the rostrum almost horizontal in the smaller male specimen, tending to be depressed at the tip in the larger female; with 8 teeth in all. Cervical sulcus interrupting the postrostral carina with a deep and wide cleft; dorsal carina prominent and flat topped and almost reaching the posterior margin of the carapace (Fig. 18A). Postrostral sulcus at least half the length of the carina, irregular in width, and widening posteriorly (Fig. 18B). Except for the postrostral carina, carapace closely similar to that of *S. choprai*. Inferior antennular flagella with approx. 100 segments and 1.5-1.9 the length of the carapace in the size range examined. Petasma and thelycum as figured by Crosnier (1978, 1989).

REMARKS. *S. koelbeli* is difficult to distinguish from *S. choprai*, the general appearance and genitalia being similar. The key distinguishing features are the relative heights of the postrostral carina, the width of the cleft at the junction of the cervical sulcus and the extent and width of the postrostral sulcus. The height of the postrostral carina is variable in *S. choprai*, sometimes approaching that of *S. koelbeli*, but the carina is usually blade-like in the former and broad and flat-topped in the latter. The postrostral sulcus is usually a series of separated elongate pits, which do not widen posteriorly in *S. choprai*, whereas in *S. koilbeli* it tends to be continuous and widens posteriorly. The cleft at the cervical sulcus is narrow in *S. choprai* and relatively wide in *S. koelbeli*.

DISTRIBUTION. Rare in Australian seas, the only records being west of Northwest Cape, approx. 200m and off the northwest shelf (depth unknown). Known range, Madagascar, Arabian Sea, Indonesia, Philippines, Gulf of Tonkin, Japan, 80-240m, rarely in shallower water down to 25m.

**Solenocera melantho** de Man, 1907
(Fig. 19A)

*Solenocera melantho* De Man, 1907: 137, 1911, 1913, pl. 5, fig. 12a-i; Starobogotov, 1972; Pérez Farfante & Grey, 1980; Crosnier, 1984, 1989, 1994; Hayashi, 1984b
*Solenocera prominentis* Kubo, 1949; Hoon Soo Kim, 1977; Lee & Yu, 1977.
*Non Solenocera melantho*, Lee & Yu, 1977.

MATERIAL. NTCR007923, M, 32mm; 4F, 39, 39.5, 41, 42mm; 007974, 4F, 37.5, 41, 43, 46mm.

DIAGNOSIS. Rostrum deep and reaching to about the extremity of the eye; with a total of 8-9 teeth, with the 4th, occasionally the 3rd above the orbital margin. Postrostral carina well defined and reaching almost to the posterior edge of the carapace; postrostral sulcus represented only by

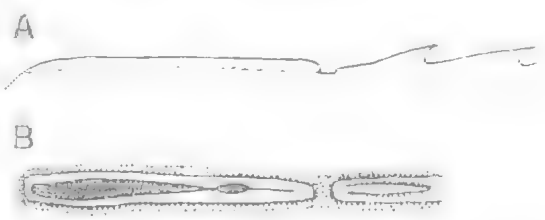



FIG. 18. *Solenocera koelbeli* de Man, 1911. WAMC25273, M, 20mm, 21°48'S 113°56'E, W of NW Cape. A, profile of postrostral carina; B, dorsal view of postrostral carina.

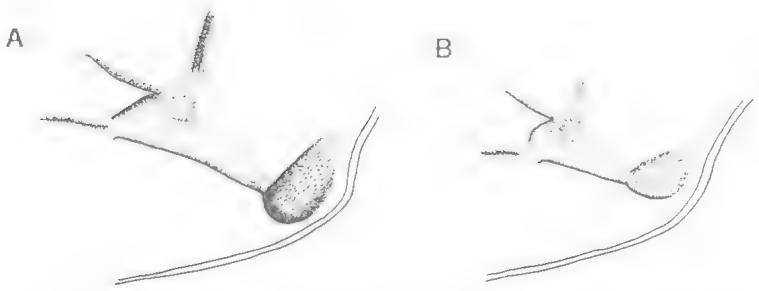



FIG. 19. A, *Solenocera melantho* de Man, 1907. Pterygostomian and hepatic region of the carapace, showing the pterygostomian pit, hepatic carina, anterior hepatic sulcus and hepatic spine. NTCR007923, F, 42mm, 9°46'S 129°54'E, 298m. B, *Solenocera australiana* Pérez Farfante & Grey, 1980. Same features as in A, QMW17419, F, 33mm, Gulf of Carpentaria, 53mm.

1-4 small pits, sometimes with none. Orbital angle sharp, antennal and hepatic spines of similar size, postorbital spine large; cervical sulcus reaching almost to the dorsum, which is only barely indented at this point. Posterior orbito-antennal sulcus deep, almost vertical and reaching the base of the postorbital spine. Anterior end of the hepatic carina curving ventrally around a deep depression at the pterygostomian angle, forming an arc, almost a semicircle (Fig. 19A). Hepatic sulcus extending posteriorly and almost joining an indistinct branchiocardiac sulcus, which nearly reaches the posterior edge of the carapace. Antennular flagella 0.9-1.25 the length of the carapace in females, longer in males and juveniles. Thelycal plate between the 5th pereopods sometimes with a low anterior median ridge, sometimes with none.

REMARKS. *Solenocera melantho* is difficult to distinguish from *S. australiana* and the features in Fig.19 and Table 3 need to be considered in conjunction when identifying these species.

DISTRIBUTION. Australian seas from Scott Reef (14°52'S 121°39'E) to the Arafura Sea (9°46'S 129°54'E), 258-298m. Known range, S Japan and N China Sea, Philippines, Indonesia and NW Australia, 150-300m.

### **Solenocera moosai** Crosnier, 1984
(Fig. 20)

*Solenocera moosai* Crosnier, 1984: 37, figs 5 a, 6 a, 7 c,d, 1989, 1994.

MATERIAL. QMW15860, 3M, 10.5, 11, 12.5mm; 17052, 5F, 12.5, 12.5, 14.5, 15, 16mm; 17053, 3F, 14.5, 16.5, 16.5mm; 17054, F, 18mm; 17055, 2F, 15, 16mm.

DIAGNOSIS. Rostrum deep proximally, sharply pointed towards the tip, with 5-6 rostral teeth in all, the epigastric widely separated from the 1st rostral tooth. Postrostral carina ending just behind a depression opposite the top of the cervical sulcus. Orbital angle absent or represented by only a low bump; postorbital spine large, antennal and hepatic spines small; posterior orbito-antennal sulcus well defined and joining a wide, shallow anterior sulcus just below the postorbital spine. Hepatic carina ending anteriorly in a sharp point, elevated above the level of the carapace, and ending posteriorly just anterior to the hepatic tooth; hepatic sulcus deep posteriorly and meeting a well-defined transverse sulcus, which runs from the lower branchiostegite to the cervical carina, defining a triangular hepatic area; branchiocardiac sulcus absent. A dorsal carina on the 3rd abdominal somite. Maximum diameter of the cornea at least 0.2 the length of the carapace. Antennular flagella 1.4-1.65 the length of the carapace in larger specimens, and 1.8 in a 12.5mm specimen. Dorsomedian lobe of petasma bilobed distally; thelycal plate of the 5th pereopods with a large low anterior boss.

TABLE 3. Principal features distinguishing *S. melantho* and *S. australiana*. Until shown to be otherwise, the last criteria are the simplest and probably the most consistent for separating the species.

| Feature | *S. melantho* | *S. australiana* |
|---|---|---|
| Rostral tooth above the orbital margin | 3rd or 4th | 4th or 5th |
| Ventral margin of rostrum | straight or slightly concave | convex |
| Anterior end of hepatic carina | almost a semicircle around a deep depression | a shallow arc around a shallow depression |
| Tip of superior antennular flagella | with a long taper | with a short taper |
| Length of adult female antennular flagella | 0.9 - 1.25 length of the carapace | 1.4 - 1.5 length of the carapace |
| Dorsolateral lobule of petasma | 1 - 13 spinules | >30 spinules |
| Thelycal plate | sometimes with anterior median ridge; posterior rim with two median setose projections | always without an anterior median ridge; posterior rim slightly concave, without median projections |
| Usual depth range | 150 - 300m | 15 - 55m |

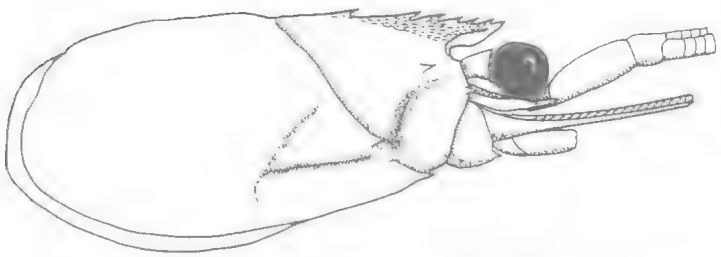


FIG. 20. *Solenocera moosai* Crosnier, 1984. QMW17052, F, 12.5mm, 17°58'S 147°06'E, 300m.

REMARKS. Crosnier (1984) notes that *S. moosai* and *S. faxoni* are closely similar and lists points of difference. The more important of these are included in the key, of which the most reliable is the small size of the eye in *S. faxoni*. Characteristics of the genitalia are additional criteria for distinguishing the two species.

DISTRIBUTION. In Australian seas, recorded only from off Tully, NE Queensland, 260-325m; probably occurs round N Australia. Known range, Makassar Strait, Indonesia (type locality); E of the Tanibar Is, Timor Sea; NE Australia; Philippines, 120-325m, mostly around 200m.

**Solenocera pectinata** (Bate, 1880)
(Fig. 21A, E)

*Philonicus pectinatus* Bate, 1888: 279, pl. 38; de Man, 1892.
?*Philonicus cervicalis* Zehntner, 1894.
*Solenocera pectinata* de Man, 1911 (p. 45, part), 1922; Balss, 1925; Anderson & Lindner, 1945; Nataraj, 1945; Hall, 1961, 1962; George, 1969 (part); Starobogatov, 1972; Crosnier, 1978, 1984, 1989, 1994b.
Non *Solenocera pectinata* de Man, 1913; George, 1967, Michel, 1974 (= *S. pectinulata* Kubo).

MATERIAL. QMW12839, M, 12mm, 3F, 14.5, 15, 15mm; 12841, F, 14.5mm; 17440, F, 12.5mm.

DIAGNOSIS. Dorsal edge of rostrum convex, with 8-9 small teeth including the epigastric; postrostral carina not extending past the top of the cervical sulcus; orbital angle blunt. Postorbital and hepatic spines of similar size, antennal spine small; cervical sulcus deep and ending just below the dorsum, which is slightly depressed at this point; posterior part of the orbito-antennal sulcus deep, its upper end reaching just above the level of the antennal spine. Anterior hepatic carina recurved, forming a blunt projection, raised above the carapace surface; the carina ending posteriorly at the tip of the hepatic tooth. Hepatic sulcus extending posteriorly to about the level of the top of the cervical sulcus; branchiocardiac sulcus barely defined. Inferior antennular flagella 1.13-1.24 the length of the carapace and with 57-63 segments. Distal third of the petasma pectinate, the ventrolateral lobe ending in a single tooth (Crosnier, 1978, fig. 61c-d); accessory lobe with 18-20 spinules (Fig. 21E). Trapezoidal plate of thelycum with a small anterior median boss, median sulcus poorly defined (Crosnier, 1978, fig. 60d-f).

REMARKS. *Solenocera pectinata* is easily confused with *S. pectinulata*, especially because the two species have similar habitats and geographical distribution (see discussion under the latter species).

Carapace colour pinkish-white; abdomen with narrow vertical red bands, blue and pink in between, uropods banded; antennular flagella white tipped, distal 2-3 segments of pereopods blue, proximal parts and pleopods pink.

DISTRIBUTION. In Australian seas from 18°42' S, off Townsville, N Queensland to the Gulf of Carpentaria, 50-100m. Known range, the Arabian Sea to Madagascar, Burma, the South China Sea, the Philippines and the Gulf of Tonkin, through Indonesia to N Australia and Wallis and Futuna Is, from near inshore to 200m.

**Solenocera pectinulata** Kubo, 1949
(Fig. 21B, C, D)

*Solenocera pectinulata* Kubo, 1949: 251, figs 8S, 27A-B, 66K-L, 72N-T, 83B, 101, 102C; Starobogatov, 1972; Crosnier, 1978, 1984, 1989; Hayashi, 1984a,b.
*Solenocera pectinata* de Man, 1911 (part); 1913, pl. 4, fig. 11; Balss, 1914 (part); George, 1967, 1969 (part); Michel, 1974.

MATERIAL. QMW12838, M, 11mm, 2F, 11.5, 12mm; 14320, M, 13.5mm, 4F, 15, 16.5, 17.5, 18mm; 15869, M, 10mm, F, 13mm; 18046, 2M, 10, 12mm, F, 18mm.

DIAGNOSIS. Rostrum acutely pointed, dorsal edge horizontal, with 6-7 prominent teeth including the epigastric; postrostral carina not extending past the top of the cervical sulcus; orbital angle barely discernible. Postorbital, antennal and hepatic spines large; cervical sulcus deep and ending just below the dorsum, which is slightly depressed at this point; orbito-antennal sulcus wide and shallow, almost reaching the base of the postorbital spine, but sometimes virtually absent. Anterior hepatic carina recurved, forming a blunt projection, raised above the

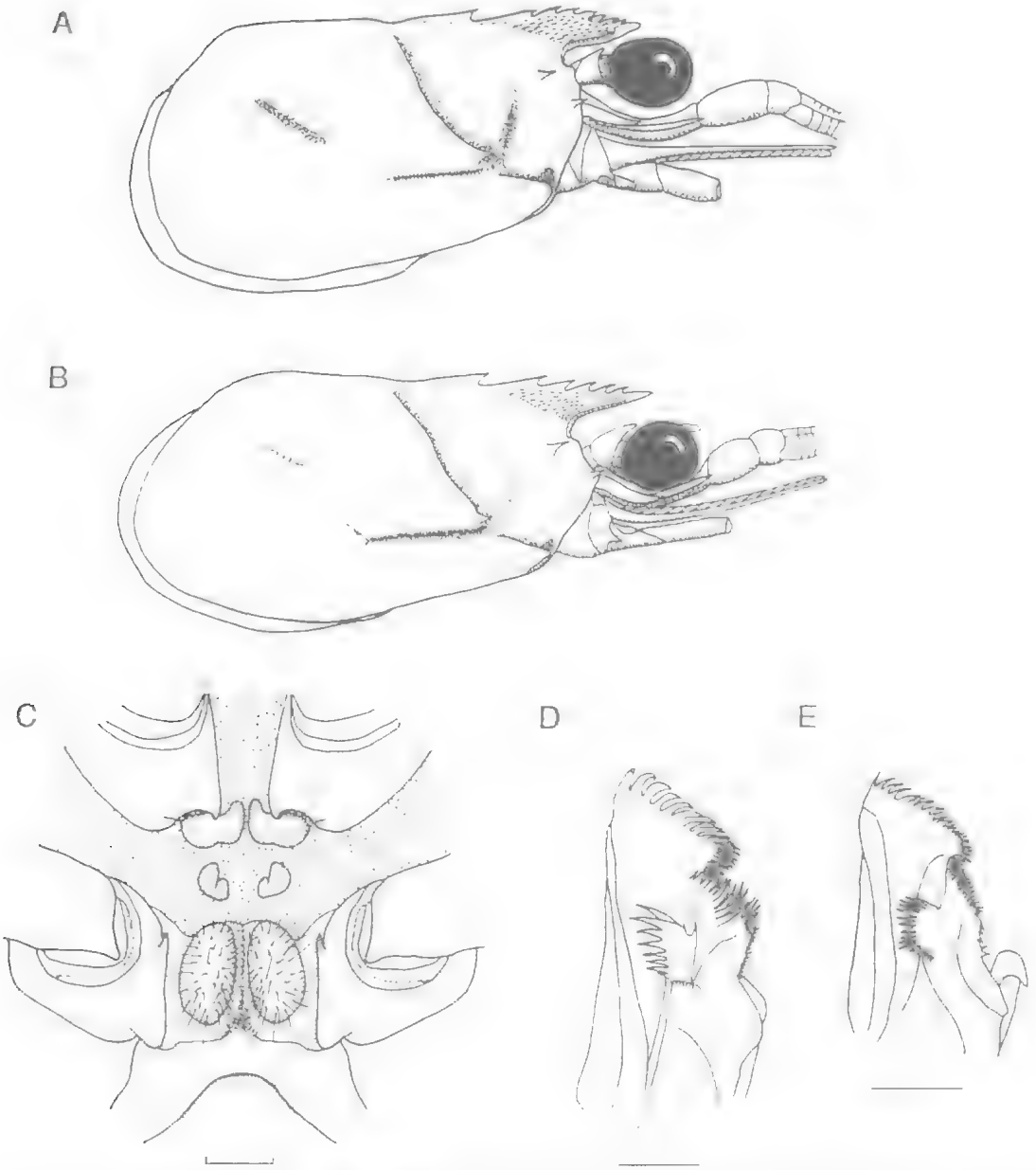



FIG. 21. A, *Solenocera pectinata* (Bate, 1880). QMW12839, M, 12mm, 18°34'S 147°09'E, approx. 75m. B, *Solenocera pectinulata* Kubo, 1949. QMW14320, M, 13.5mm, off Mission Beach, depth unknown. C, *Solenocera pectinulata*, thelycum, QMW14320, F, 18mm (scalebar = 1mm). D, *Solenocera pectinulata*, petasma, distal right half, external aspect, showing accessory lobule, QMW14320, M, 13.5mm. E, *Solenocera pectinata* (Bate, 1880), similar details to D, QMW12839, M, 12mm (A).

carapace surface; the carina ending posteriorly at, or just in advance of the tip of the hepatic tooth. Hepatic sulcus extending posteriorly a little behind the level of the top of the cervical sulcus; branchiocardiac sulcus virtually absent. Antennular flagella 0.9-1.0 the length of the carapace and with 44-53 segments. Distal third of the petasma pectinate, the ventrolateral lobe ending in two teeth (Crosnier, 1978, fig. 61a-b); accessory lobule with about eight large spinules (Fig. 22C). Trapezoidal plate of thelycum with a

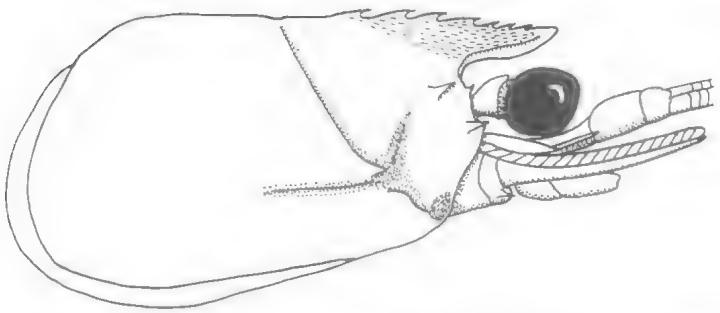


FIG. 22. *Solenocera rathbuni* Ramadan, 1938. NTCR007941, F, 13mm, 19°28'S 118°29'E, 52m.

well defined median sulcus, running between a pair of prominent ovoid bosses (Fig. 22B).

REMARKS. As mentioned above, *Solenocera pectinulata* is difficult to distinguish from *S. pectinata*, especially without the other species for comparison. Also, the antennular flagella, one of the best means of separating the two species, are often missing. The features of Table 4, taken together, will usually give a reliable identification.

DISTRIBUTION. In Australian seas from NE Queensland, from Innisfail to Townsville, 50-200m. Known range, Japan, Philippines, Indonesia, N Australia, W coast of India to Madagascar, 75-350m, mostly above 175m.

**Solenocera rathbuni** Ramadan, 1938
(Fig. 22)

*Solenocera lucasii*, Rathbun, 1906: 904, pl. 20, fig. 9; Burkenroad, 1934.
*Solenocera rathbuni* Ramadan, 1938: 57; Starobogatov, 1972; Ivanov & Hassan, 1976; Crosnier, 1978, 1989, 1994b; Kensley, Tranter & Griffin, 1987.

MATERIAL. QMW14304, M, 20mm; NTCR00624, 3M, 12, 12, 15mm, 3F, 16.5, 17, 18mm; 007941, 4F, 12, 13, 13, 16mm.

DIAGNOSIS. Rostrum deep and reaching about half the cornea, strongly convex ventrally and with a total of 7-8 teeth. Postrostral carina ending opposite the top of the cervical sulcus. Orbital angle sharp, antennal and hepatic spines small, postorbital spine large. Cervical sulcus deep and almost reaching the dorsum, which is scarcely depressed at this point. Anterior end of hepatic carina forming a shallow arc around the ventral side of a shallow depression near the pterygostomian angle. Hepatic sulcus extending posteriorly to about the level of the top of the cervical sulcus; branchiocardiac sulcus virtually absent; orbito-antennal sulcus shallow and not reaching the base of the postorbital spine. Dorsomedian and dorsolateral lobules of the petasma pectinate with long teeth; ventrolateral lobule with a single large tooth. Thelycal plate between the 5th pereopods largely enclosed by two blade-like inner projections of the coxae; thelycal plate with an anterior rounded boss and two lateral conical bosses, the 3 forming a triangle.

REMARKS. *Solenocera rathbunii* is relatively featureless but is closest to *S. waltairensis* which has not yet been reported from Australian waters; the key features appear to be the best for separating the two species.

Carapace colour red to pink with whitish patches; abdomen with narrow red dorsal bands, edged with white; antennular flagella red and white tipped, other appendages red, mostly with some white.

DISTRIBUTION. In Australian waters from SE Queensland to NW Australia, 50-200m. Known range, South of Madagascar, Philippines, Australia, Hawaian Is, Wallis and Futuna Is, 26-440m.

## ZOOGEOGRAPHY OF THE SOLENOCERIDAE IN THE INDO-WEST PACIFIC

The four principal families of the Penaeoidea in the Indo-West Pacific are the Penaeidae, Solenoceridae, Aristaeidae and Benthesicymidae (the fifth family, the Sicyonidae, is poorly represented). The species of the Penaeidae are largely inhabitants of inshore areas and the continental shelf. The limits to their distribution are largely determined by temperature, larval advection, oceanic deeps and coastal geography (Dall et al., 1990; Dall, 1991). About half of the Penaeidae are endemic to various sub-regions, but those species living at greater depths generally have a wide distribution. This is also evident in the Aristaeidae and Benthesicymidae, which are deep water inhabitants and mostly have a cosmopolitan distribution (Crosnier, 1978, 1985; Crosnier & Forest, 1973). The Solenoceridae lie between these 2 extremes with 17 of the 45 authentic Indo-West Pacific species apparently with a limited distribution. Some of this may be an artifact. Unless a species is

TABLE 4. Features distinguishing *S. pectinata* and *S. pectinulata*.

| Feature | *S. pectinata* | *S. pectinulata* |
|---|---|---|
| Rostral teeth | 8-9, small | 6-7, large & prominent |
| Dorsal edge of rostrum | slightly convex | straight |
| Inferior antennular flagella | > 57 segments, 1.3-1.24 length of carapace | 44-53 segments, 0.9-1.0 length of carapace |
| Distal end of ventrolateral lobe of petasma | 2 teeth | 1 tooth |
| Accessory lobule of petasma | about 8 large spinules | 18-20 spinules of varying size |
| Trapezoidal plate of thelycum | a small anterior median boss; median sulcus ill-defined | no anterior median boss; median sulcus well-defined, separating a pair of large bosses |

common, its apparent distribution may be a function of the extent and intensity of deep-water trawling. With few exceptions, only scientific expeditions trawl below 1,000m and thus species occurring below this depth may appear to be correspondingly rare e.g. *Gordonella* species and two of the three *Haliporus* species. With this proviso it is possible to draw some conclusions about the general distribution of the Solenoceridae.

Lower temperature is an obvious limiting factor to the Penaeidae. The Solenoceridae, being mainly inhabitants of deeper waters, with more uniform temperatures, could be expected to be less influenced by this, but existing records of their distribution show that they are confined within thermal limits similar to that of the Penaeidae, that is, the 15°C minimum winter sea surface temperatures. Like the Penaeidae, the number of species attenuates with increasing latitude outside the tropics, except that in the Solenoceridae the attenuation is not as marked. In Australia 10 out of 57 species (18%) of Penaeidae, compared with 10 out of 26 species (38%) species of Solenoceridae, occur outside the tropics. Since the Penaeidae are mostly shallow-water tropical species their thermal restriction is explicable. In contrast, the distribution of the deeper-water Solenoceridae appears to be something of a paradox. The water temperatures at 400m between 40°N and 40°S latitude range between approx. 9° and 15°C and vary little with latitude or season, the higher temperatures being localised and due to the influence of warm water oceanic eddies (Sverdrup et al., 1970). At higher latitudes the temperatures at 400m begin to fall appreciably and in the southern hemisphere the Subtropical Convergence zone begins at around 40°S. Temperature may also limit the vertical distribution of the Solenoceridae. Only two *Gordonella* and two *Haliporus* species are adapted to depths below 1,500m and most solenocerids live above 900m where the temperature exceeds 5°C (Sverdrup et al., 1970). It may be that it is the temperature of intermediate waters that determine the range of the solenocerids. This temperature limitation also suggests that the Solenoceridae were tropical in origin and have retained the need for warmer water at some stage of their life cycle. Advection of vertically migrating larvae of shallow-water Penaeidae can be significant (Dall et al., 1990), and could also contribute to the limitation of distribution of the Solenoceridae, but virtually nothing is known of their larval ecology.

The other possible barriers to distribution in the Penaeidae are oceanic deeps and coastal geography (Dall, 1991). Oceanic deeps would only have the effect of restricting species to their preferred depth range. Geography of the continental shelf and slope could be an effective barrier, for example, an extensive change from the soft substrates inhabited by *Solenocera* species to rubble or rock.

Of the 16 solenocerid species recorded with limited distribution, some are probably artifacts due to their rarity. It is unlikely, for example, that a species recorded only in the Strait of Malacca would not occur throughout Indonesia, the Philippines and the South China Sea. Eliminating those rare species with probable more extensive geographic ranges leaves seven: four from SE Africa – Madagascar, *Cryptopenaeus catherinae*, *Haliporoides triarthrus*, *Hymenopenaeus furici*, *Solenocera africana*; three from the Australian region, *Haliporoides cristatus*, *Solenocera australiana* and *S. bifurcata*. In this latter region true endemic species are very probably *Solenocera australiana*, a shallow water species and *Haliporoides cristatus*, limited to the east coast. Both are abundant species. *Solenocera bifurcata* is so far rare and is limited to the east coast, but is a relatively shallow water species and thus could be a true endemic species.

There appears to be a barrier to the Penaeidae to the NW of Australia, either due to the Timor Trench or adverse currents or a combination of both (Dall, 1991). This barrier would also be effective to *Solenocera australiana*, which is a continental shelf species, not occurring below

70m. On the west coast the most southern record of a solenocerid is 30°S, not far from the latitude of the 15°C minimum winter isotherm. On the east coast, the southward East Australian Current extends the limit of solenocerid distribution to 38°S, also the latitude of the 15°C minimum winter isotherm. Combined with New Guinea, however, the East Australian Current tends to limit migration to the north (Dall, 1991). Thus there are three endemic species of Penaeidae on the east coast and on present evidence two Solencoceridae.

From the Australian point of view, perhaps the most significant aspect of solenocerid distribution is that Australia, far from being deficient, contains well over half the known species in the Indo-West Pacific.

## ACKNOWLEDGEMENTS

I thank the Director of the Queensland Museum for appointing me an Honorary Research Fellow, which gave me access to the Museum's facilities and enabled me to commence this research. I am grateful to Peter Davie, Curator of Crustacea, and his assistant, John Short for their assistance at all times. I also thank the Chief, Division of Marine Research, CSIRO for providing laboratory space and facilities at the Cleveland Marine Laboratories. I thank the following: Karen Coombes, Collections Manager of the Museum and Art Gallery of the Northern Territory for her helpfulness and promptness in forwarding specimens, which much extended the scope of this work; Peter Arnold, Museum of Tropical Queensland, for forwarding rare specimens; Melissa Hewitt, Assistant Curator and Alison Sampey, Technical Officer, Western Australian Museum for providing data of collections and forwarding specimens. Finally, I would particularly thank Alain Crosnier, Muséum National d'Histoire Naturelle for critically reading this manuscript and providing unpublished data on various museum specimens.

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**FIRST RECORD OF FALSE KILLER WHALES (*PSEUDORCA CRASSIDENS*), IN NEW CALEDONIA, SOUTH PACIFIC.** *Memoirs of the Queensland Museum 43(2): 588.1999:*- On September 14, 1996, at 10:07 a group of false killer whales, *Pseudorca crassidens*, was observed in the waters of the SW limit of the lagoon surrounding New Caledonia (22°33.8'S, 166°59.0'E). Observations were carried out during an annual humpback whale, *Megaptera novaeangliae*, research season. Sea conditions were very calm, visibility was hazy with over 75% cloud cover. The sea surface temperature taken at 09:00 was 22.75°C.

The animals were swimming towards the SE when first sighted and did not deviate from this path when approached in a 5m outboard boat. The group was large, comprising more than 100 individuals and consisting of many subgroups containing between 5 and 10 individuals each. The subgroups were at least 20m apart and spread over a large area of the sea surface. This type of schooling behavior is consistent with other observations of this species (Acevedo-Gutiérrez et al., 1997; Leatherwood & Reeves 1983), known for it's gregarious behavior (Stacey & Baird, 1991).

The animals were approximately 5m in length, a great deal larger than the pygmy killer whale, *Feresa attenuata*, or the melonhead whale, *Peponocephala electra* (Jefferson et al., 1993). While the heads of the animals were rounded, they lacked the pronounced melon of short-finned pilot whales, *Globicephala macrorhynchus* (Jefferson et al., 1993), and had no obvious beak. Their dorsal fins were pointed but curved and around 20-30cm in height. For some individuals the ventral coloring was slightly paler than the rest of the animal, which was a dark gray. Field notes describing physical characteristics and photographs (Fig. 1) leave no doubt about the identification of the animals as false killer whales, *Pseudorca crassidens*.

Whistles emitted by the false killer whales were audible from the boat with the motors running, with the aid of a hydrophone both whistles and sonar clicks could be heard. A 22-minute recording of the false killer whale was made. For the entire period of the recording animals continued to pass the boat. At one stage 4 individuals approached and swam under the boat turning sideways as they passed, sonar clicks became very strong at that moment.

On departing in the same direction as the false killer whales, a subgroup of 5 individuals approached the boat and began surfing the bow wave. Using a crossbow and adapted bolt a biopsy was taken from a large individual. While with this subgroup, other subgroups were continuously visible, some containing smaller individuals assumed to be juveniles. These groups never approached the boat.

The continuous passage SE of the subgroup accompanying the boat was interrupted at 11:16 when they paused on the surface. One individual made a sudden, and extremely rapid, movement out of the subgroup. Five minutes later an individual was observed carrying a large piece of yellowfin tuna, *Thunnus albacares*, in it's mouth. While the dietary habits of false killer whales are not well known, they appear to feed opportunistically on a wide range of prey types and sizes, including large pelagic species such as Mahi-mahi, *Coryphaena hippurus* (Leatherwood & Reeves, 1983; Stacey & Baird, 1991).



FIG. 1. False killer whale *Pseudorca crassidens*, demonstrating the characteristic rounded head lacking a beak and the tall, falcate dorsal fin.

After catching the tuna the subgroup started to distance itself from the boat. Avoidance behavior was initiated by diving for a period of about two minutes, after which the subgroup surfaced 50m in front of the boat and several breaches were observed. We accelerated to a speed of 6 knots to follow the subgroup. The remaining contact with the group consisted of them surfacing at 2-minute intervals while moving steadily towards the southeast. Boat speed varied between 3.3 and 10.8 knots. At midday it was decided to stop following the group, the final position was 22°36.3'S, 167°04.8'E. We had remained with the group for 1 hour 53 minutes, covered a distance of approximately 6.4 nautical miles and traveled at an average speed of almost 5 knots.

Reports of false killer whales from the SW Pacific are not uncommon, mass strandings of the species have been recorded from both New Zealand and Australia (Baker, 1983). In addition, this species has been caught incidentally in Taiwanese gillnets from N Australia (Harwood et al., 1984), and reported from dolphin drive fisheries in the Solomon Islands (Dawbin, 1974). In spite of a few records from inshore waters (Stacey & Baird, 1991; Acevedo-Gutiérrez et al., 1997), the false killer whale is known as a pelagic species (Wade & Gerrodette, 1993), so it is not surprising that sightings have not been more frequent in New Caledonia, where most scientific studies are confined to the inner lagoon. It is likely that this species is not uncommon in the oceanic waters surrounding the New Caledonian lagoon.

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# FOLIVORY AND BILL MORPHOLOGY IN THE TOOTH-BILLED BOWERBIRD, *SCENOPOEETES DENTIROSTRIS* (PASSERIFORMES: PTILONORHYNCHIDAE): FOOD FOR THOUGHT

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Frith, C.B. & Frith, D.W. 1999 06 30: Folivory and bill morphology in the Tooth-billed Bowerbird, *Scenopoeetes dentirostris*, (Passeriformes: Ptilonorhynchidae): food for thought. *Memoirs of the Queensland Museum* **43**(2): 589-596. Brisbane. ISSN 0079-8835.

The Tooth-billed Bowerbird, *Scenopoeetes dentirostris*, is a facultative, arboreal, folivore. For a substantial proportion of winter diet they tear and masticate pieces of leaves, succulent buds and vine stems, but in summer they are mostly frugivorous. Specialised notches, cusps, or 'teeth' on their lower mandible cutting edges fit into reciprocal indentations in the upper mandible when the bill is closed, to more efficiently crush and masticate vegetable matter. As a result of this diet, birds commonly void compact faecal 'pellets' consisting predominantly to exclusively of finely-masticated foliage. Folivory by this passerine in the resource-rich habitat of tropical upland rainforest is surprising and may be in part due to the presence in its habitat of three closely related bowerbird, and many other frugivorous, species. Studies of Tooth-bill diet, nutrition, and associated morphology and physiology are required.
❒ *Folivory, bill morphology, bird 'teeth', mastication of foliage, Tooth-billed Bowerbird, Scenopoeetes dentirostris.*

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The Tooth-billed Bowerbird, *Scenopoeetes dentirostris* (subsequently Tooth-bill), represents a monotypic genus of the bowerbird family, Ptilonorhynchidae, whose 19 species are endemic to Australia and Papua New Guinea. It occurs only in upland rainforests between 600-1400m above mean sea level, from Mt Amos (15°42'S 145°18'E), near Cooktown, southward to Mt Elliot (19°30'S 146°57'E), just south of Townsville, N Queensland, tropical NE Australia (Nix & Switzer, 1991). Tooth-bills, like other polygynous bowerbirds, demonstrate male promiscuity and female-only nesting duties. They are, however, atypical in being sexually monomorphic, short and stout-billed, and in court-clearing males that form exploded leks (Frith & Frith, 1985a, 1993, 1994, 1995).

Male Tooth-bills clear leaf litter to form a display area on the forest floor about the base of at least one tree trunk and collect fresh large leaves to lay them paler side uppermost on this court. Courting starts with singing and court maintenance from late August to September and continues to January or early February (see Frith & Frith, 1993, 1994).

Jackson (1909, 1910), Marshall (1951, 1954) and Warham (1962) made preliminary studies of males and courts, and limited knowledge of nesting biology is summarised by Frith & Frith (1985a). Geoffrey Moore (unpubl. data) examined the role of males as plant seed dispersal agents. Court seasonality, morphology, dispersal, constancy and ownership are detailed in Frith & Frith (1994) and home range in adult males in Frith et al. (1994).

The Tooth-bill is unique among bowerbirds in having a conspicuous irregular notch or 'tooth' on the cutting edges of the upper mandible and several, more regular, cusps and notches on the tip and cutting edges of the lower mandible respectively. These 'teeth' were long considered adaptations used solely to obtain leaves for court decoration, by biting, snipping or sawing at their petioles (Marshall, 1951; Gilliard, 1969; Chaffer 1984). In support of this interpretation Marshall (1954) and Chaffer (1984) noted that the means by which Tooth-bills obtained leaves for the court was laborious and arduous; birds having to tear and saw at leaf petioles, particularly those of larger ones such as the gingers (*Alpinia* spp.). A fully-developed 'toothed' bill adorns birds of both sexes and all post-juvenile ages, while only older males (probably > 2-3 years old, pers. obs.) decorate courts with leaves.

By far the most commonly used leaves for court decoration at Paluma, near Townsville, N Queensland were those of the small tree *Polyscias australiana* (see Frith & Frith, 1994),

but this is not necessarily the case elsewhere (pers. obs.). Leaves of *P. australiana* are quickly and and easily removed from the plant by male Tooth-bills. It is possible that differing leaf attachment strengths of plants accounts for the observed differences in Tooth-bill effort in leaf removal.

Recent observations have demonstrated that Tooth-bills are partly folivorous and that the externally-toothed bill is an adaptation to this diet (Lavery & Grimes, 1974; Frith & Frith, 1979 and unpubl. data). Tooth-bills certainly use the 'tooth-like' structures of the mandible edge to cut, tear, and manipulate leaves and leaf pieces (Lavery & Grimes, 1974). However, between these external serrations lie a more sophisticated and complex set of structures, alluded to by Marshall (1954: 154) whose function equates more closely to that of 'teeth'. This contribution provides an initial description of these structures of bill and palate and illustrates graphically how they function to finely masticate foliage prior to ingestion. We do not review comprehensively the morphology, ecology, nutrition or physiology associated with this unusual passerine diet. Our aim in presenting this review of our initial findings is, as the subtitle implies, to stimulate the interest of appropriate specialists in these aspects of Tooth-bill biology.

## METHODS

We studied male Tooth-billed Bowerbird sociobiology and ecology from 1978 to 1990 in rainforest near Paluma (19°00'S 146°10'E), N Queensland at an elevation of ~875m ASL. Subsequent qualitative work was carried out on the Atherton Tableland (17°25'S 145°42'E ~ 680m ASL). Intensive annual fieldwork began as soon as males started singing and/or clearing and decorating courts (September or early October at Paluma); and annual fieldwork ceased when singing and court usage declined (during January or early February). Court attendance, displays and vocalisations were monitored intensively from 7 November to 8 December 1979 and 1 October 1980 to 14 February 1981 (see Frith & Frith, 1993, 1994, 1995; Frith et al., 1994). To learn what male Tooth-bills ate during their court-attendance season we erected ~50cm$^2$ pieces of black nylon fine mesh ~10cm above the forest floor beneath low (<1.5m) court perches favoured by males. Excreta voided by birds from these perches accumulated on the nylon and were collected weekly for subsequent analysis (Frith & Frith, 1994 & unpubl. data). As males spent on average 64% of daylight upon such favoured perches during their peak display season (Frith & Frith, 1994, 1995) faecal samples were large. Because Tooth-bills swallow whole the vast majority of fruits they eat (larger figs, *Ficus* spp, excepted) seeds are intact, and no regurgitation occurs, these samples represent an accurate indication of fruit diet. In addition to work on males at courts, the feeding ecology of the species was examined by recording all observed bowerbird foraging during 1,360hrs of standardised transect and quadrat observation and an additional 187h of random observation through Tooth-bill habitat. These observations resulted in 533 records of Tooth-bills feeding upon plants.

Subsequent to the report that Tooth-bills eat foliage by tearing leaves, buds and vine stems and manipulating and masticating them prior to ingestion (Lavery & Grimes, 1974; Frith & Frith 1979), we closely examined the bill of several living and preserved Tooth-bills for physical adaptations to such folivory.

## RESULTS

Tooth-bill folivory typically involved a quietly perched solitary bird biting or tearing off pieces of fresh leaf or vine stem growth. Once a larger piece of leaf was removed from the plant it was rapidly, skillfully and repeatedly 'folded' in the mandible tips into a compact wad. This was then masticated or 'chewed' between the mandible tips before being ingested; green fluid resulting from the mastication often visibly accumulated at the tip of the mandibles (Frith & Frith, 1979) and presumably with some ingested.

The majority of Tooth-bill excreta accumulated beneath favoured court perches consisted of an amorphous mass (with some, more recently produced, discrete faecal 'pellets') of fruit pericarp and seeds, the quantity of this increasing during seasonal peak court attendance (Frith & Frith, 1995). Some 5 to 10% of monthly excreta samples consisted of faecal 'pellets' predominantly or exclusively composed of finely-masticated vegetable matter (see Figs 1 & 2A). The smaller samples of such faecal matter for Oct-Dec, compared with Sept, 1979 are due to lower court attendance levels by males due to unseasonally dry conditions (Frith & Frith, 1994). It must be noted that the percentages in Fig. 1 for leaf matter are minimal because we scored each entire pellet of same as one 'leaf' record whereas the remaining mass of fruit

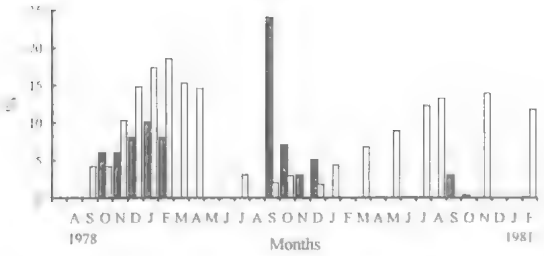



FIG. 1. Percentage of total weekly excreta samples, collected beneath court perches favoured by court-attending male Tooth-billed Bowerbirds, consisting of faecal pellets primarily of masticated leaf matter (solid bars) and the percentage of sampled trees that were bearing fruit (open bars) over three courtship seasons (see text).

remains were scored by constituent fruits (as indicated by seed numbers). While these data were only obtainable during the months that males attended courts they do suggest an increase in folivory when fewer fruits were available in the habitat (see Fig. 1, text below, and Frith & Frith, 1995, 1998).

While details of direct observations of Tooth-bill foraging will be presented elsewhere, we note that of 533 records of feeding upon plant material observed, 79% were upon fruits and 21% (n = 111) upon other plant material as follows: leaves (n = 90), flowers (8), succulent stems (7) and buds (6). We stress that we consider this 21% of annual diet as folivory to be a gross underestimate, because Tooth-bills eating foliage (particularly during winter when they become silent, secretive and inactive in the forest canopy) are extremely cryptic while birds taking fruit are much more conspicuous because fruiting plants attract numerous bowerbirds and other frugivorous birds (pers. obs.).

During winter, Tooth-bills become so elusive that some observers believed they left their upland rainforest breeding habitat (e.g. Green, 1910). As a percentage of directly-observed Tooth-bill foraging events, folivory increased during periods of least fruit availability within the habitat (Fig. 1). The percentage of directly observed folivory was >20% but at times may reach 25-40% (Fig. 3) which, for winter months at least, we consider an underestimate (as above). The gizzard of a male Tooth-bill that died on 14 June 1989 contained 7.8g of finely-masticated leaf mash (see Fig. 2b); the entire gut being full of finely-textured green leafy slime.

## DISCUSSION

FOLIVORY. Habitual folivory is a rare trait among birds. However, the New Zealand avifauna is exceptional in this regard, having evolved in the absence of competion from browsing mammals (I. Flux, pers. comm.). A notable terrestrial and arboreal folivore is the flightless, nocturnal, Kakapo, *Strigops habroptilus*, an extraordinary parrot endemic to New Zealand temperate forests which browses plants by masticating leaves and fronds, often in situ on some plants (Merton, 1985). Elsewhere folivory is common typically among the non-passerine groups of: waterfowl, which feed upon aquatic vegetation or graze upon terrestrial grasses and herbage; some terrestrial game bird groups including the palearctic Black Grouse, *Tetrao tetrix*, and Western Capercaillie, *Tetrao urogallus* (Phasianidae), (Dorst, 1974); some rails; and several other species (Dorst, 1974: 70; Morton, 1978; Carboneras, 1992; Taylor, 1996). True folivory is also well known in the extraordinary, neotropical, Hoatzin (*Opisthocomus hoazin*, an aberrant cuckoo) that lives in riverine gallery forest subject to flooding (Dominguez-Bello et al., 1994; Thomas, 1996)

Folivory is particularly rare among arboreal passerines. It is known, however, as typical foraging in the three neotropical plantcutters (*Phytotoma* spp., Cotingidae: Küchler, 1936; Ames, 1971; Lanyon & Lanyon, 1989; Sibley & Ahlquist, 1990) of open woodland and scrub (Ridgely & Tudor, 1994) and in three species of saltator (*Saltator* spp., Emberizidae) of secondary growth, gardens, plantations and forest edge (Jenkins, 1969; Stiles & Skutch, 1989). The Kokako (*Callaeas cinerea*, Callaeidae) of New Zealand temperate forests is conspicuously folivorous and will eat yellowing, dehiscent, or even brown and dead, leaves of some plants (Hay, 1985; I. Flux, pers. comm.; pers. obs.). It is also known in the Common Bullfinch, *Pyrrhula pyrrhula* (Fringillidae), and several other species (Dorst, 1974) which eat buds more than leaves, but is otherwise only occasionally observed as an irregular and small dietary component in few passerine species (i.e. some birds of paradise and bowerbirds: Frith & Frith, 1979; Donaghey, 1981, 1996; Frith & Beehler, 1998). It is doubtless more widespread than is indicated by present knowledge.

It has been noted that Hoatzin selectively eat 'young leaves, tender shoots and buds, which are higher in water content, as well as being both

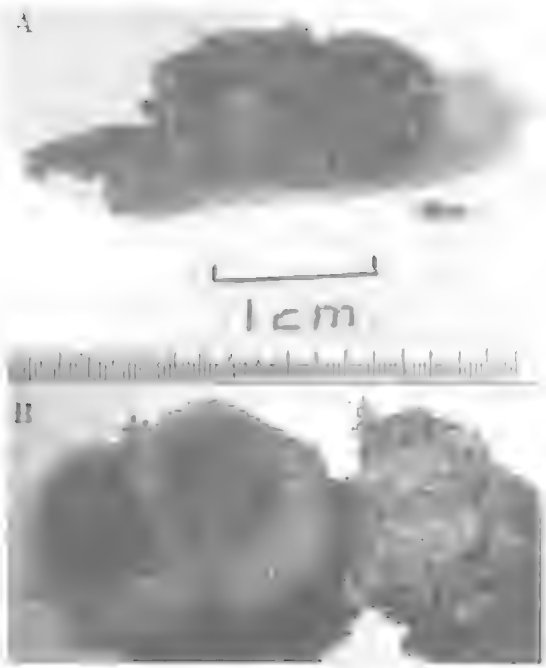



FIG. 2. A, fresh Tooth-billed Bowerbird faecal pellet consisting predominantly of finely-masticated leaf matter with 1cm scale indicated. B, freshly dissected Tooth-billed Bowerbird gizzard (left) and its content (right) of finely-masticated leaf matter (ruler with 1 and 5mm markings). Both near Paluma, Queensland, June 1989.

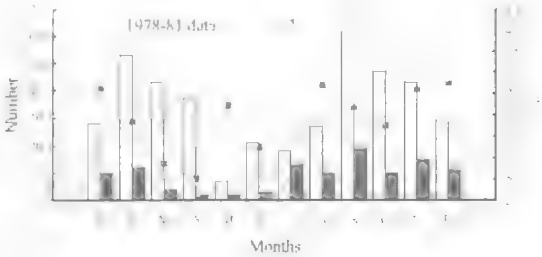



FIG. 3. Number (left axis) of observations of Tooth-billed Bowerbird feedings near Paluma, Queensland, upon fruit (open bars) and foliage (solid bars), and the percentage (right axis) records of foliage eating represented of total feeding events during each month (line curve with solid squares). Data for August 1978-February 1981 inclusive are combined.

easier to digest and more nutritious' (Thomas, 1996). This statement applies equally to the Tooth-bill in our experience. The Hoatzin is remarkable, however, in that its crop and lower oesophagus are its main digestive organs. Hoatzins ferment vegetation in the foregut in a similar way to the gut fermentation of cattle (Strahl et al., 1989; Dominguez-Bello et al., 1993; Thomas, 1996). Physiological adaptations to the digestion of such an unusual and presumably low carbohydrate/energy diet, such as an (if only seasonally) elongated gut (see Sibly, 1981), might be expected. These have not, however, been looked for in Tooth-bills, or in the several other bowerbird species which also eat foliage to a lesser extent. We did not investigate the relative nutritional values of plant foliage eaten by Tooth-bills, and this remains a field for future study.

Foliage represents a dietary component low in readily available carbohydrate/energy content (Sun et al., 1997; Powlesland et al., 1997). The energetic disadvantage of small body size probably limits folivory in passerines, this diet being far more common in larger birds and especially those with fewer predators. That this rare avian diet and associated bill adaptations occur in the Tooth-bill begs the obvious question: why so in this passerine? It is possible that lower fruit resource availability in winter has resulted in the need for obligate frugivores to perform folivory as an adaptation to winter survival, but supporting data are few (Figs 1 & 3; Frith & Frith, 1998, fig. 2c). An adequate answer will doubtless require considerable research and time. It has been noted that the extraction of energy from leaves requires a relatively long food retention time and that large quantities must be ingested and stored; circumstances which present major disadvantages for flying animals (Morse, 1975; Morton, 1978; Sibly, 1981). An alternative strategy is for rapid throughput of plant material with minimal digestion (Sibly, 1981). The Tooth-bill remains markedly inactive and apparently flies little during the winter months, when folivory quite possibly dominates its diet. Thus the low energetic demands of eating (abundant) leaves might outweigh the costs of seeking (sparse) winter fruits. As predator pressure may be important in explaining why folivory is rare in birds (Morton, 1978), particularly in passerines, the highly cryptic plumage and folivorous foraging of both sexes of the Tooth-bill are noteworthy.

Satin Bowerbirds, *Ptilonorhynchus violaceus*, form flocks in the winter to early spring and then, typically, eat terrestrial herbs and grasses in both rainforest and woodland (Donaghey, 1981; Vellenga & Vellenga, 1985; pers. obs.). These plants may represent a seasonally significant proportion of their diet (c. 50-80% according to

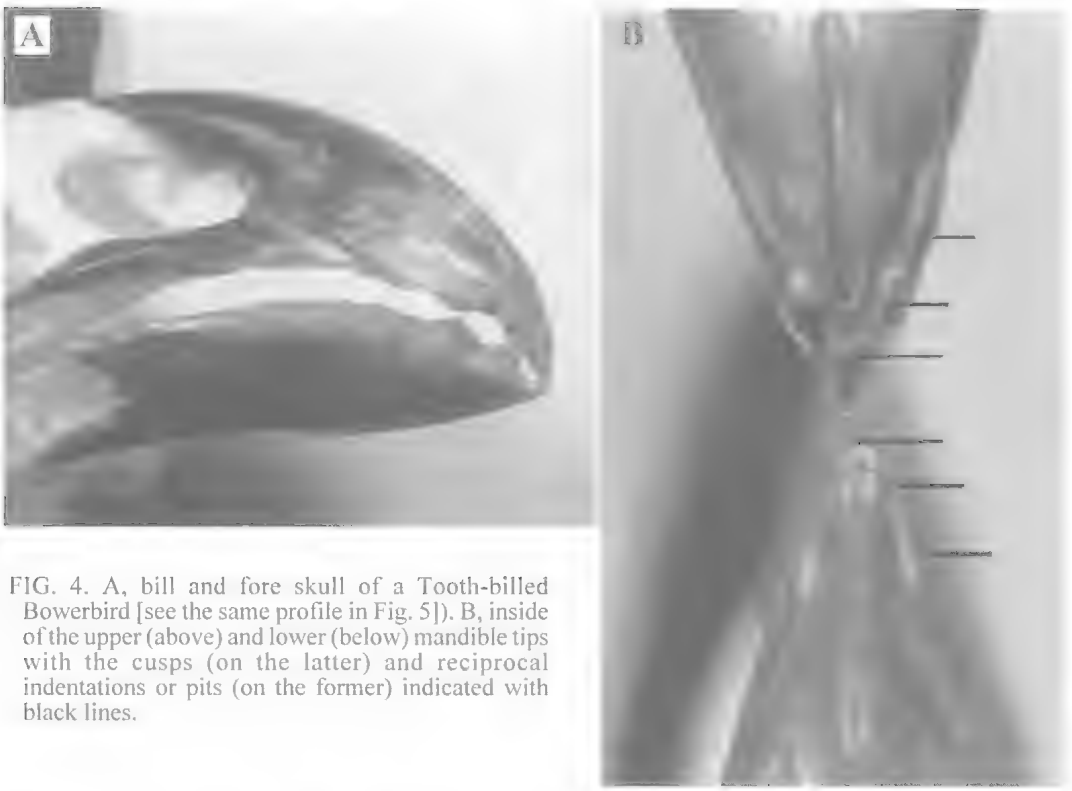



FIG. 4. A, bill and fore skull of a Tooth-billed Bowerbird [see the same profile in Fig. 5]). B, inside of the upper (above) and lower (below) mandible tips with the cusps (on the latter) and reciprocal indentations or pits (on the former) indicated with black lines.

Donaghey, 1981). Satin Bowerbirds appear to 'chew' leaf matter in the mandible tips prior to ingesting it. Male Satin Bowerbirds (and other avenue bower building species) also masticate foliage to produce 'paint' which they apply to the inner surface of bower walls (Marshall, 1954; Gilliard, 1969; Donaghey, 1996; pers. obs.). It should be noted, however, that Satin Bowerbirds, including those populations (*P. v. minor*) sympatric with Tooth-bills do so in habitats adjacent to, but outside, the rainforsts within which Tooth-bills perform their winter folivory (Frith & Frith, unpubl. data).

Donaghey (1981, 1996) found that Satin Bowerbirds living in subtropical woodland ate more leaves during winter to early spring, than those living in adjacent rainforest, suggesting that the latter area was richer in other foods. As tropical rainforests are rich in diverse avian food resources it is surprising to find substantial folivory in the Tooth-bill. The Tooth-bill is sympatric with three, predominantly frugivorous bowerbirds (Spotted Catbird, *Ailuroedus melanotis*, Satin Bowerbird and Golden Bowerbird, *Prionodura newtoniana*) and a number of other, obligate, frugivores. This may have played some role in the evolution of its folivory through interspecific competition (Lack, 1971; Lavery & Grimes, 1974), particularly during strong competitive pressure exerted by lean seasons. In the upland wet tropical rainforest habitat of the Tooth-bill, the winter months are resource-poor with respect to both arthropods (Frith & Frith, 1985b; Frith, D. & Frith, C., 1990), which female Tooth-bills feed to their offspring as a small proportion of their diet, and fruits (Frith & Frith, 1994). Such a scenario might, in addition to a lack of predators, have in part influenced the evolution of partial folivory in the New Zealand Kokako as this (now endangered) passerine shared much of its habitat with two, predominatly insectivorous, closely related members of the same family (the Saddleback, *Philesturnus carunculatus* and the, now extinct, Huia, *Heteralocha acutitostris*). The folivorous, and now endangered, flightless Kakapo similarly shared habitat with up to four other New Zealand endemic parrot species.

BILL MORPHOLOGY. With respect to fruits, Tooth-bills are 'gulpers' (Levey, 1990) in that they swallow fruits whole with their seed(s) intact, do not typically use their 'teeth' to remove

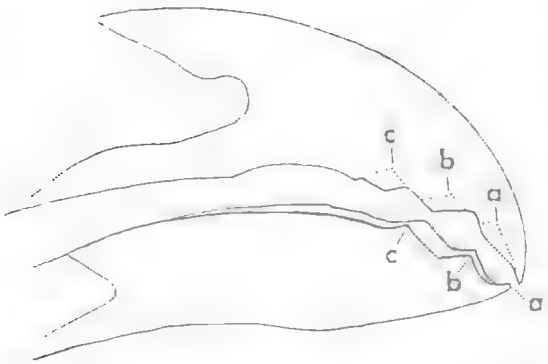



FIG. 5. A simplified schematic diagram of a Tooth-billed Bowerbird bill in profile showing how the cusp at the tip of the lower mandible (lower a) and those on its cutting edges (lower b & c) fit into the reciprocal indentations (dotted lines) in the upper mandible (upper a,b &c) when the mandibles are closed to masticate foliage. See also Fig. 4.

flesh of large-seeded fruits, and do not regurgiate seeds. The more easily digested nutrients, of proteins and soluble carbohydrates, in plant foliage cells are protected by cellulose walls which vertebrates lack the enzymes to digest, and the cell walls must therefore be mechanically broken up (Sibly, 1981). Details of direct observation of feeding Tooth-bills combined with knowledge gained by examination of several preserved and living individuals suggest to us that: a) the cutting edges of the reciprocal mandibular notches (Fig. 4a) are used to bite or tear and then manipulate and fold leaf pieces into a compact wad prior to mastication, and that b) the lower mandible 'teeth', used in a 'chewing' action, enhance digestibility of foliage by crushing and grinding. Thus the 'teeth' serve to break up the cell walls of the foliage. The nature of voided faecal 'pellets' of masticated leaf matter (Fig. 2a) suggest that Tooth-bills might not digest plant fibre, as does the Hoatzin, but merely break down plant cells and so release their digestable content; but this requires experimental study. Certainly male Tooth-bills at their courts do not regurgitate indigestable fibre as do many frugivores.

The most important point concerning the Tooth-bill's use of lower mandibular 'teeth' is that their five functional tips, or cusps, fit perfectly into reciprocal indentations, or pits, in the under surface of the distal premaxilla (see Figs 4, 5). These specialised structures form efficient grinding 'teeth' for Tooth-bills by creating pressure points for foliage mastication (Fig. 6). Notwithstanding their folivory, there is no comparable sophistication of bill morphology in Satin Bowerbirds.

Various bill modifications to deal with vegetable matter are known in the waterfowl (Johnsgard, 1968) and some other groups (see above). We were able to briefly examine a freshly-thawed Kokako specimen while in New Zealand in May 1998 and found structures on the central palate of the upper premaxilla that may function in mastication of vegetable matter. However, this possibly novel adaptation awaits confirmation in additional specimens, and an understanding of its function, and formal description (I. Flux, pers. comm.).

It is noteworthy that the considerable literature on the Hoatzin and its folivorous diet does not appear to allude to any kind of mastication of vegetation or to morphological adaptations of the inner mandibles for doing so (Thomas, 1996 & references therein). However, the cutting edges



FIG. 6. Part of the base of a *Polyscias australiana* leaf found freshly laid upon a Tooth-billed Bowerbird court as a court decoration. Note that the 'bruise' marks left by the bird's bill clearly indicate the pressure points where the five lower mandible cusps meet the reciprocal indentations (indicated) in the upper mandible (see Figs 4, 5).

of the mandibles of the three neotropical plant-cutters are conspicuoulsy serrated, presumably to enhance their cutting (and masticating?) function. While many of the pan-tropical (Australasia excluded) non-passerine barbets (Piciformes, Capitonidae) show a diversity of conspicuously notched or 'toothed' mandible edges, no evidence to suggest these might be used in folivorous feeding appears to exist notwithstanding long-term intensive collecting and observation of African and Asian species. A recent review of diets of all African species makes no mention of foliage found in birds or seen to be eaten by them (Short & Horne, 1988). The Great Barbet, *Megalaima virens*, has a long but visibly unnotched or 'toothed' bill but has, however, been noted to avidly eat flower petals by 'the whole flower being first revolved and crushed in the mandibles and compacted into boluses of crumpled petals' (Ali & Ripley, 1970). The same authors note that the Green Barbet, *M. zeylanica*, eats flower petals.

We suggest that the mandibles and palate of specimens of all folivorous birds, and any suspected of being so, be examined for the possible presence of structures for the mastication of foliage as this might prove instructive. There can be no doubt that studies of Tooth-bill diet, nutrition, and associated morphology and physiology will prove rewarding in the broad context of avian folivory.

## ACKNOWLEDGEMENTS

We are most grateful to Alan Tennyson and Ian Flux of Wellington, New Zealand, for the opportunity to discuss Kokako ecology and to examine a specimen in the flesh. We particularly thank Ian Flux, Eugene Morton, Peter Woodall and an anonymous referee for kindly commenting constructively on a draft of this contribution.

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# A NEW FRINGED STARGAZER (URANOSCOPIDAE: *ICHTHYSCOPUS*) WITH DECRIPTIONS OF THE OTHER AUSTRALIAN SPECIES

MARTIN F. GOMON AND JEFF W. JOHNSON

Gomon, M.F. & Johnson, J.W. 1999 06 30: A new fringed stargazer (Uranoscopidae: *Ichthyscopus*) with descriptions of the other Australian species of the genus. *Memoirs of the Queensland Museum* **43**(2): 597-619. Brisbane. ISSN 0079-8835.

*Ichthyscopus nigripinnis* sp. nov. is described from a series of specimens collected off the northeastern coast of Australia extending from northern New South Wales to eastern Papua New Guinea. The species appears most closely related to *I. spinosus* from northern Western Australia, with which it shares a highly developed subcleithral ridge and a partially separated anterior portion to the dorsal fin, but resembles *I. barbatus* from southern Australia more closely in coloration. The new species is distinguishable from the former by the absence of dark spots on the upper portion of the head and body and the presence of fimbriae on the horizontal fleshy ridge adjacent to the upper pectoral fin base. It is separable from the latter by its well defined, jet black anterior segment of the dorsal fin and the absence of barbels on the midline of its chin. Detailed descriptions of Australian congeners, *I. barbatus*, *I. fasciatus*, *I. insperatus*, *I. sannio* and *I. spinosus*, are also presented. A cladistic analysis of the interrelationships between Australian species of *Ichthyscopus* based on 14 variable characters supports two similar trees of equal length. An evolutionary hypothesis is presented for Australian *Ichthyscopus* based on this analysis, the current distributions of species and perceptions of past climatological fluctuations. ❐ *Uranoscopidae, Ichthyscopus, Stargazer, Australia.*

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The Australian region is remarkable for its high diversity and endemicity of fishes belonging to a large number of widely distributed marine families. The stargazer family Uranoscopidae is a good example, and no genus demonstrates it better than *Ichthyscopus* Swainson. In his study of the relationships of members of the family, Pietsch (1989, based on Mees, 1960) indicated that the genus 'apparently contains five species', all of which occur in Australia and four of which are confined to its waters. A recent examination of Australian stargazers has revealed the presence of yet another endemic species of *Ichthyscopus* and has shed further light on the interrelationships of taxa in this genus.

Mees (1960) reviewed *Ichthyscopus*, along with other Australian uranoscopid genera known to him at the time. Three additional species of *Ichthyscopus* and a comparison of Whitley's (1936) *I. sannio* with *I. lebeck* (Bloch & Schneider, 1801) were presented. The study has since been regarded as the definitive treatment of the genus but provides only minimal descriptions of even Mees' taxa. The purpose of this paper is to present a description of a recently detected sixth Australian species of *Ichthyscopus*, to provide more detailed descriptions of its 5 Australian congeners, and to comment on the interrelationships of the species currently recognised in the genus and the associated biogeographical implications.

## METHODS

Counts, measurements and terminology mostly follow Hubbs & Lagler (1947). The body depth was measured at the origin of the dorsal fin, following Bruss (1986). The head width was taken at the middle of the operculum. Orbital diameters were recorded both as longitudinal and transverse measurements. The eye diameter is the longitudinal dimension. The interorbital distance refers to the distance between the mesial rims of the left and right orbits at the center of the orbit, while the interorbital fossa width is the distance across the interorbital fossa at the level of the center of the orbit. The length of the cleithral spine was measured along the axis of the spine from its tip to the point it disappears beneath the opercle.

The anatomical form of the elements (spines versus soft rays) at the anterior end of the dorsal

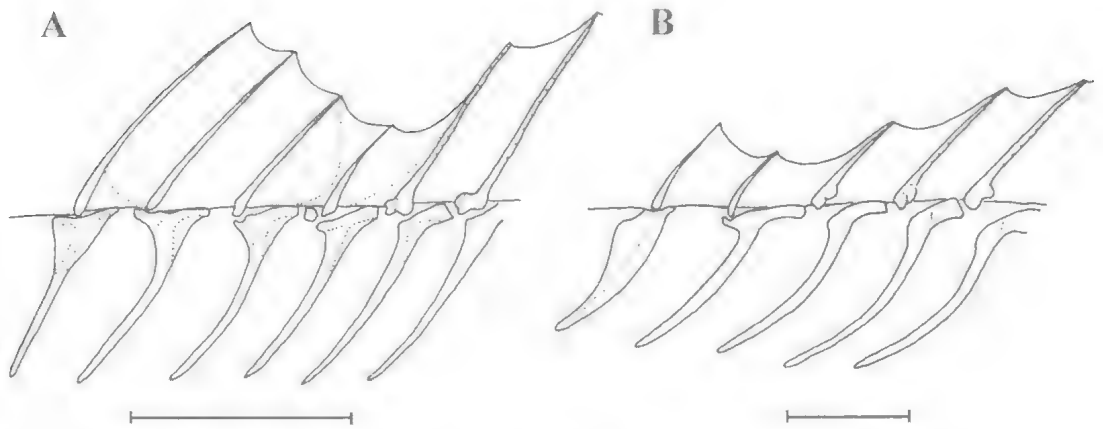



FIG. 1. Anterior end of dorsal fin with associated proximal pterygiophores in: (a) *Ichthyscopus nigripinnis*, holotype, QM I30217, 110mm SL, and (b) *I. barbatus* SAM388, 196mm SL. Scale bars = 10mm.

fin is extremely difficult to recognise on external examination, or for that matter, with the use of radiographs. Consequently, though the number of spines regularly separates this species from congeners, it is of dubious use as a key character. Spines and soft rays do appear to be consistent in their relation to supporting proximal pterygiophores, with spines regularly carried anteriorly above the upright shaft of the pterygiophore and soft rays articulating with a posterior extension of the 'head' of the proximal pterygiophore (Fig. 1). The last dorsal spine and first soft ray of the dorsal fin are supported by the same pterygiophore. The first soft ray may also be recognised by its expanded cap-like proximal end. Values of '.5' in reference to dorsal and anal fin formulae refer to a small ray-like element close behind the otherwise last ray of the fin. In most cases the former is associated with a small proximal pterygiophore and may represent a complete, albeit small ray, and not a branch of the terminal ray separated to the base as occurs in many other higher bony fishes. The extremely fleshy nature of fin coverings makes the accurate determination of supporting element numbers impossible without the use of radiographs or clearing and staining techniques. Although radiography is useful for revealing the fin ray compliments of unpaired fins, the technique will not show the numbers of elements in paired fins because of underlying bony structures. An examination of cleared and stained material indicated that external counts on pectoral fins are likely to miss the dorsalmost hair-like modified first ray positioned closely in front of the rather short unbranched 2nd ray. Likewise, the spine of each pelvic fin is short, embedded at the base of the fin and virtually invisible from external examination. Scale row counts include smaller scales in less well defined rows on upper corner of caudal peduncle.

Institutional acronyms used to denote collections in which examined specimens are lodged follow the standardised list of Leviton et al. (1985). Numbers enclosed by parentheses following catalogue numbers in lists of type specimens and material examined refer to the number and size range (mm SL) of specimens. In the detailed description of the new species, information pertaining to the holotype is presented first and variations observed in paratypes follow in parentheses. Meristic values for internal features were obtained using lateral radiographs. Values for pleural ribs have been omitted as anterior elements were obscured by the pectoral fin and its basal skeleton in those specimens examined. Pietsch (1989) reported the genus to have 2 or 3 ribs anteriorly and 1 posteriorly. This study confirms that Australian species of the genus consistently have a pair of pleural ribs associated with the haemal spine of the 2nd caudal vertebra, but does not record the number and positions of ribs anteriorly.

Selected meristic and morphometric characters are provided for 6 species of *Ichthyscopus* in Table 1. The 14 variable characters listed in Table 2, with the character states occurring in the 6 Australian species of *Ichthyscopus* and the more primitive uranoscopid genus *Uranoscopus* (as determined by Pietsch, 1989), were compared using PAUP computer software to derive the most parsimonious hypothesis of relationships.

## KEY TO AUSTRALIAN SPECIES OF *ICHTHYSCOPUS*

1. Outer surface of cleithral spine almost entirely exposed, ventrally fringed fleshy covering confined to lower margin, not extending posteriorly beyond spine tip; approximately 52-84 obliquely angled scale rows on sides; body with 5 or 6 equally spaced, broad dark bands dorsally . . . . . *I. fasciatus*

   Cleithral spine entirely enveloped by ventrally fringed fleshy covering, extending as tapered flap well posterior to spine tip; scales absent or in 28-59 (rarely more than 53) obliquely angled rows on sides; body with dark bands, saddles, spots or mottling dorsally, but not as described above . . . . . 2

2. Body without scales; body dorsally with 5 dark edged saddles (small specimens) or with 9 or 10 dark edged vertical bands (large specimens) . . . . . *I. insperatus*

   Body with scales appearing as obliquely angled folds along sides of body; body dorsally with 2 dark saddles, numerous dark spots or dark and pale mottling . . . . 3

3. Fimbriae on lips with 1 or 2 rows of evenly spaced lateral branches on either side in adults; each side of lower jaw with 12-21 rather short conical teeth; dorsal portion of body dark with distinctly pale mottling . . . . *I. sannio*

   Fimbriae on lips without lateral branches in adults; each side of lower jaw with 4-14 prominent slender canines, posteriormost often noticeably longer than those anteriorly; dorsal portion of body with dark saddles or spots . . . . . 4

4. Crest of horizontal fleshy subcleithral ridge anterior and posterior to upper end of pectoral base irregular, sometimes with simple papillae but lacking branched fimbriae (Fig. 2A); numerous small dark spots on upper portion of sides and head . . . . . *I. spinosus*

   Crest of horizontal fleshy subcleithral ridge anterior and posterior to upper end of pectoral base with numerous, often laterally branched fimbriae (Fig. 2B); each side of body with 2 large dark saddles or blotches dorsally . . 5

5. Dorsal fin rather dark anteriorly, its distal margin slightly concave (Fig. 1B); midline of chin with vertically aligned pair of small fleshy barbels; skin flap adjacent to ventrolateral edge of lower lip with smooth margin (Fig. 3B); posterior nostril circular (Fig. 4B); inner surface of pectoral fin almost uniformly dusky with pale distal margin and pale fleshy base . . . . . *I. barbatus*

   Dorsal fin black anteriorly, an anterior segment separated from rest of fin by a deep concavity (Fig. 1A); midline of chin without barbels; skin flap adjacent to ventrolateral edge of lower lip with arborescent margin (Fig. 3A); posterior nostril ovoid, rimming fleshy anterior gap in bony orbit (Fig. 4A); inner surface of pectoral fin with pale rays and dark intervening membrane . . . . . *I. nigripinnis* sp. nov.

### **Ichthyscopus nigripinnis** sp. nov.
(Figs 1A, 2B, 3A, 4A, 5-7, 8A)

ETYMOLOGY. *nigripinnis*, an amalgamation of the Latin adjective *nigra* for 'black' or 'dark', and noun *pinna* for 'fin', in reference to the partially separated black anterior segment of the dorsal fin characterising this species.

MATERIAL. HOLOTYPE: QMI30217 (1, 110) Queensland, Moreton Bay, 4 miles NE of Mud I., 27°17'S 153°18'E, 15m, 1 November 1994, Qld DPI Fisheries. PARATYPES: AMSIA1392 (1, 137) Qld, Bowen, registered 6 July 1923, E. Raniford; AMS IB2957 (1, 208) Papua New Guinea, Laloki R., L. Jones; AMS I20212-015 (1, 41.6) Qld, One Tree I. Lagoon, 23°30'S 152°05'E, 18-20m, 6 October 1971; AMSI 25425-001 (1, 135) NSW, off Ballina, 28°52'S 153°40'E, 36m, 14 February 1966, NSW Fisheries; AMS I31476-007 (2, 100-124) NSW, off Murwillumbah, 28°20'S 153°40'E - 28°25'S 153°41'E, 54-58m, 2 May 1990, FRV Kapala, K. Graham; AMSI31484-001 (1, 137) NSW, off Brunswick Hds, 28°26'S 153°41'E - 28°25'S 153°41'E, 53-57m, 16 February 1991, FRV Kapala, K. Graham; AMSI33571-001 (1, 81.9) NSW, off Iluka, 29°23'S 153°23'E - 29°44'S 153°23'E, 23-28m, 7 May 1990, FRV Kapala, K. Graham; AMSI33669-001 (1, 89.7) NSW, off Iluka, 29°22'S 153°23'E - 29°21'S 153°24'E, 25-28m, 14 November 1991, FRV Kapala, K. Graham; AMSI33681-001 (1, 116) NSW, off Brunswick Hds, 28°23'S 153°38'E - 28°25'S 153°38'E, 47-51m, 24 March 1992, FRV Kapala, K. Graham; AMSI37479-001 (1, 119) NSW, off Iluka, 29°49'S 153°20'E - 29°50'S 153°21'E, 34-37m, 26 May 1995, FRV Kapala, K. Graham; NMVA20079 (1, 50.4) NSW, off Iluka, 29°23'S 153°24'E - 29°22'S 153°25'E, 29-31m, 18 April 1996, FRV Kapala, K. Graham; NMVA20080 (1, 54.8) NSW, SE of Yamba, 29°39'S 153°21'E - 29°38'S 153°21'E, 25-33m, 11 September 1995, FRV Kapala, K. Graham; QMI4252 (1, 162) Qld, Moreton Bay, 3 November 1925, W. Hiddens; QMI9521 (1, 113) & QMI9522 (1, 84) Qld, Gneering Shoals, off Mooloolaba, 26°40'S 153°13'E, 36.5m, 2 February 1961, J.M. Moulton; QMI9983 (2, 86-89) Qld, 5-6 miles east of Point Cartwright, 26°40'S 153°13'E, trawl 34.7-38.4m, 5 March 1970, F. Wallace; QMI10754 (1, 100) Qld, off Maroochydore, 26°41'S 153°14'E, 25.6m, coarse sand, 29 November 1950, E.M. Grant; QMI11823 (1, 103) Qld, Northumberland Group, 20.1-54.8m, 8 August 1957, FRV Challenger, N. Haysom; QMI11908 (1, 275) Qld, Heron I., 23°27'S 151°55'E, 30 January 1951, C. Cox; QMI17169 (1, 70) Qld, Tongue Reef, 16°26'S 145°45'E, 3m, 27 October 1974, B.L. Scomazzon. OTHER MATERIAL: QMI17079 (1, 270) Qld, 7 miles east of Mooloolaba, 26°41'S 153°16'E, 29.2m, coarse sand, 30 September 1979, J. Johnson (otoliths only).

DIAGNOSIS. Dorsal fin with 3 (rarely 4) spines and 16-17.5 soft rays, the anterior end differentiated by a deep concavity in the distal margin (Fig. 1A), 4th element (usually = 1st soft ray) shortest, anterior segment distinctively black with white basal margin at least anteriorly and posteriorly; opening of posterior nostril elongate, ovoid, rimming fleshy anterior gap in bony orbit (Fig. 4A); labial fimbriae simple, smooth-edged; skin flap adjacent to ventrolateral edge of lower lip with one to numerous, simple to palmate fimbriae on margin (Fig. 3A), especially near corner of mouth; each side of lower jaw with 4-9 teeth; chin lacking barbels; cleithral skin flap nearly twice length of cleithral spine; fleshy

TABLE 1.Observed ranges for selected morphological dimensions (as percent of standard [SL] or head lengths [HL]) and meristic characters in Australian species of *Ichthyscopus*.

| | *I. nigripinnis* | | *I. barbatus* | *I. fasciatus* | I. *insperatus* | *I. sannio* | *I. spinosus* |
|---|---|---|---|---|---|---|---|
| | holotype | paratypes | | | | | |
| No. of specs : standard length | 110 | 22: 41.6-275 | 11: 118-237 | 5: 102-243 | 6: 33.0-177 | 24: 45.0-431 | 2: 134-165 |
| Body depth / SL | 37.6 | 33.1-42.8 | 30.0-35.8 | 25.2-32.9 | 31.2-34.6 | 29.5-37.1 | 34.4-39.5 |
| Head length / SL | 36.9 | 30.6-42.3 | 29.0-34.2 | 30.8-34.7 | 30.7-37.9 | 30.9-36.9 | 36.1-41.3 |
| Head width / SL | 36.2 | 29.9-37.3 | 32.4-38.5 | 28.1-30.8 | 28.2-36.9 | 31.0-38.1 | 33.8-41.7 |
| Orbital diameter (long) / HL | 18.5 | 14.1-20.6 | 12.6-19.2 | 15.3-19.1 | 17.5-20.0 | 13.1-18.7 | 15.9-17.1 |
| Orbital diameter (transv) / HL | 16.5 | 11.3-18.9 | 11.4-15.8 | 11.3-14.1 | 12.5-15.9 | 10.2-16.1 | 12.5-14.3 |
| Eye diameter / HL | 11.8 | 7.9-14.4 | 8.2-12.7 | 8.6-11.2 | 10.3-14.4 | 5.7-12.7 | 10.2-10.8 |
| Interorbital distance / HL | 19.9 | 17.1-24.3 | 25.4-28.5 | 17.7-20.2 | 20.0-28.9 | 20.6-27.4 | 20.1-23.8 |
| Interorbital fossa width / HL | 13.0 | 9.8-16.8 | 12.4-23.1 | 6.2-8.7 | 9.1-13.6 | 11.2-19.8 | 14.3-19.6 |
| Cleithral spine length / HL | 15.3 | 14.4-30.9 | 21.8-31.9 | 21.7-27.4 | 28.0-30.6 | 23.8-36.5 | 15.7-19.3 |
| Head shield length / HL | 31.8 | 28.1-37.7 | 34.4-41.9 | 42.3-53.0 | 34.4-42.6 | 24.6-33.5 | 27.1-29.0 |
| Pectoral fin length / SL | 32.6 | 27.9-35.2 | 28.5-34.4 | 23.7-30.2 | 29.0-38.2 | 27.0-33.6 | 29.9-32.1 |
| Pelvic fin length / SL | 26.0 | 20.0-30.5 | 21.7-28.8 | 17.2-19.2 | 22.6-27.3 | 22.4-26.2 | 23.7-27.2 |
| Dorsal fin | III, 16.5 | III-IV,16.5-17.5 | II, 17-17.5 | I, 17.5-20 | I, 18-19 | II-III, 16-17.5 | II, 17.5 |
| Anal fin | 16.5 | 15-16.5 | 16-16.5 | 17-18.5 | 16-17 | 16.5-17.5 | 16 |
| Pectoral fin | 14 | 13-16 | 13-15 | 15-16 | 14-15 | 17-18 | 16-17 |
| Vertebrae | 9 + 17 | 9 + 17-18 | 9 + 17-18 | 9 + 18 | 9 + 16-17 | 9 + 18 | 9 + 16 |
| Epipleural ribs | 11 | 7-11 | 8-11 | 9 | 8-9 | 7-9 | 8 |
| Upper lip fimbriae | 16 | 15-22 | 17-23 | 23-26 | 19-34 | 27-36 | 25-26 |
| Lower lip fimbriae | 50 | 38-56 | 41-52 | 38-45 | 44-49 | 41-51 | 52-55 |
| Lower jaw teeth | 4, 5 | 4-9 | 2-9 | 11-18 | 9-14 | 12-21 | 4-9 |
| Opercular fimbriae | 23, 24 | 16-29 | 21-31 | 11-18 | 15-26 | 12-19 | 21-23 |
| Cleithral flap fimbriae | 20, 21 | 15-24 | 21-28 | 8-14 | 15-21 | 15-22 | 15-18 |
| Scale rows | 46 | 36-51 + 0-9 | 28-45 + 0-10 | 52-84 | 0 | 47-59 | 38-41 |

horizontal subcleithral ridge continuing on posterior side of pectoral fin axis to just below free posterior tip of cleithral skin flap, forming free pointed flap posteriorly; crest of ridge fimbriate anterior and posterior to pectoral fin base; fimbriae similar in structure to those on opposing margin of cleithral flap; scales present, in 36-51 oblique rows; sides dusky dorsally, each with two large dark blotches, positioned below anterior and posterior ends of dorsal fin; pectoral fin with distinctive pale rays and black intervening membrane.

DESCRIPTION. Dorsal fin rays III, 16.5 (III or IV, 16-17.5; anterior elements slender, 4th usually an unsegmented, unbranched 'soft ray' which is difficult to distinguish from preceding spines even with use of radiographs; 5th usually segmented but unbranched; last element often smaller than penultimate element and may or may not be associated with a reduced pterygiophore making it difficult to determine if it is separate or simply a ray branched to the base); anal fin rays 16.5 (15-16.5, usually 16.5; last element as in dorsal fin); caudal fin with 12 (rarely 13) principal rays and 3 (3 or 4) unsegmented procurrent rays dorsally and ventrally; pectoral fin rays 14 (13-16; 1st element unbranched); pelvic fin rays I, 5 (spine a short spur concealed in thick skin and closely associated with 1st ray); branchiostegal rays 5;

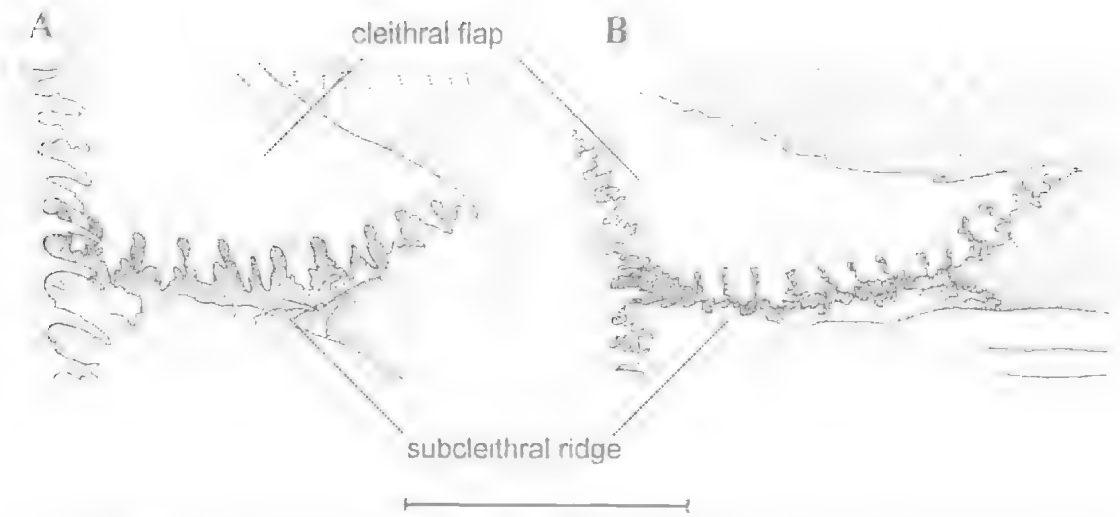



FIG. 2. Cleithral region (left side) showing fleshy subcleithral ridge in A, *Ichthyscopus spinosus*, NTMS10959-020, 134mm SL, and B, *I. nigripinnis*, AMSI37479-001, 119mm SL. Scale bar = 10mm.

vertebrae 9+17 (rarely 9+18); epipleural ribs 11 (7-11, mean 9.05), situated on vertebra 4-14 (4 or 5 - 11 to 14).

Body moderately deep, compressed posteriorly; head rather square in cross section see Table 1 for morphometric data.

Head mostly encased in bone, without obvious joint lines dorsally (Fig. 6); bony surface textured with fine low vermiculations; dorsal surface mostly flat, only slightly concave posterior to interorbital fossa. Interorbital fossa rectangular, width posteriorly only slightly less than that between orbits. Orbit circular, diameter distinctly greater than that of eye. Anterior nostril small, approximately 1/4 eye diameter, tubular, partially divided into 2 openings by midposterior flap; anterior side with low rim providing notch, rim edged with moderately short simple fimbriae. Opening of posterior nostril elongate, ovoid, rimming fleshy anterior gap in bony orbit; nostril with prominent anterior flap and less prominent medial and lateral flaps, each with fimbriate edges; anterior flap functionally dividing nostril into lateral and mesial openings. Both lips with simple, smooth edged fimbriae externally, fimbriae on lower lip occasionally branched at corner of mouth; 16 (15-22) individual fimbriae on upper lip, 50 (38-56) on lower; skin flap on lower jaw adjacent to ventrolateral edge of lower lip with one to many, simple to palmate fimbriae on margin, especially near corner of mouth; inner edge of upper and lower lips also with fimbriate fringe. Upper jaw with broad band of numerous small slightly curved teeth; teeth not in distinct rows, about 3 or 4 teeth across band where broadest. Lower jaw in large specimens with 4 or 5 widely spaced straight prominent narrow canines angled back into mouth on each side, posteriormost noticeably longer than others (smaller specimens with up to 8 or 9 teeth on each side of lower jaw). Oral valve broad, fleshy, drawn upwards into a low point medially (one specimen with simple fimbriate margin). Chin smooth, without barbels. Dorsal half of opercular margin fimbriate, with 23 or 24 (16-29) individual fimbriae; ventralmost simple, those dorsally with up to 8 simple lateral branches, branches rarely subdivided; opercular margin smooth ventrally.

Cleithral spine extending posteriorly almost to above dorsal extent of pectoral fin axis. Fleshy cleithral skin flap enveloping spine extending well past this point; underside of flap fimbriate with 20 or 21 (15-24) individual fimbriae, including several simple fimbriae anteriorly beneath opercular margin; fimbriae, including that at tip of flap, with up to 9 side branches on both anterior and posterior margins, those closest to tip with the most branches; branches only occasionally subdivided into sub- branches (occurring most often proximally on flap); occasionally 1 or 2 simple fimbriae on dorsal edge of flap near tip. Narrow fleshy subcleithral ridge extending horizontally from upper angle of opercular opening to dorsal extent of pectoral fin base, continuing on posterior side of pectoral fin axis to just below free posterior tip of cleithral skin flap, forming free pointed flap posteriorly; crest of ridge fimbriate anterior and posterior to

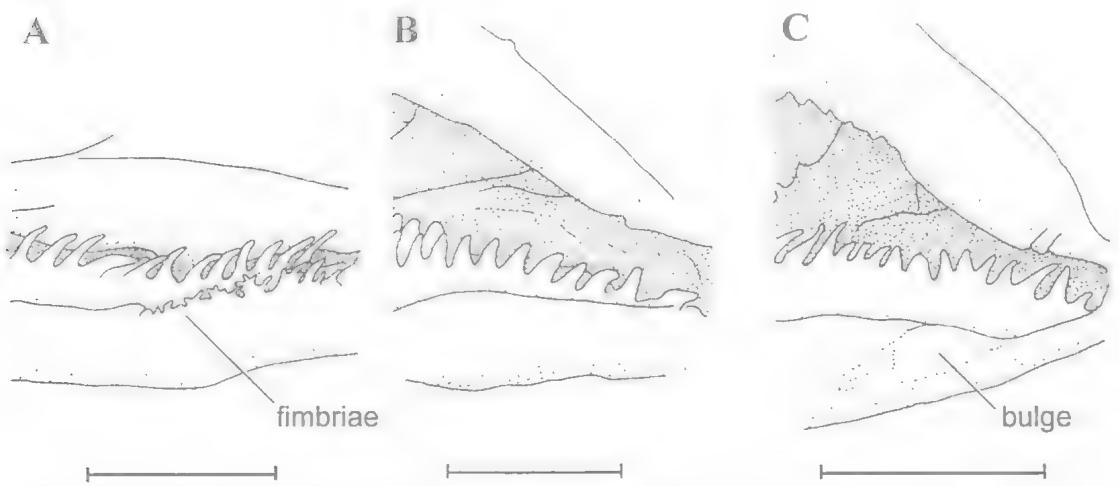



FIG. 3. Corner of mouth (left side) showing margin of skin flap adjacent to ventrolateral edge of lower lip in A, *Ichthyscopus nigripinnis*, AMSI33681-001, 116mm SL, B, *I. barbatus*, NMVA13018, 130mm SL, and C, *I. insperatus*, WAMP1858-001, 115mm SL. Scale bars = 5mm.

pectoral fin base; fimbriae similar in structure to those on opposing margin of cleithral flap (Fig. 2B). Upper half of opercle and preopercle with low surface vermiculations similar in form but finer in texture than those on dorsal cranial plates; lower halves with simple fine striae radiating ventrally. No spines associated with subopercle, opercle, preopercle or basipterygium.

Dorsal fin rather long-based and low, anterior end partially separated into short anterior segment by deep concavity; first 4 (4 or 5) dorsal fin elements relatively short, 1st longest, 4th (4th or 5th) shortest, 4th about half length of 1st and 6th. Anal fin long-based and low. Caudal fin truncate to slightly rounded with branched tips of caudal rays extending slightly beyond membrane. Pectoral fin pointed, tip of 3rd ray at point, membrane incised slightly between tips. Pelvic fins strong and fleshy, inner 2 rays longest, interradial membranes more clearly incised in remaining rays. Ventral midline with medial ventral skin flap from anterior tip of basipterygium to rear of pelvic fin base. A small rounded transverse flap posteriorly at midbase of pelvics.

Scales prominent, cycloid, rectangular, arranged in about 46 (36-51, usually 46 or 47) obliquely angled rows, occasionally two scale rows merging into one as they proceed ventrally (one specimen with scale rows on one side of body obliquely ventrad to about eleventh dorsal ray and obliquely dorsad at rear, other side of same individual with typical obliquely ventrad scale pattern); additional scales scattered on caudal base (up to 5 scales of various sizes horizontally along patch); peduncular scale rows from posterior end of anal base to distal corner of peduncle 14 (13-16). Underside of body naked anteroventral to a line between tip of cleithral skin flap and center of anal fin base. Lateral line pores in angled lines or clumps of 3-8 at dorsal end of each diagonal scale row. Nape between rows of lateral line pores devoid of scales except for a few embedded scales in a single row just mesial to row of lateral line pores on either side; sensory pores absent from nape except for those associated with lateral line, those on naked skin adjacent to posterior margin of head shield and those piercing head shield posterolaterally.

Colour in alcohol (Fig. 5) brownish grey dorsally on sides and head, creamy white below with two pairs of broad dark blotches, one below lateral line at origin of dorsal fin and behind upper end of operculum, extending onto upper edge of cleithral flap ventrally; second pair saddle-like, on and beneath posterior end of dorsal fin, extending well ventrally. Opercle, preopercle and much of maxilla creamy white; remainder of cheek, upper lip, lower lip and chin brownish grey. Dorsal fin brownish grey except for prominent black anterior segment and somewhat darker posterior saddle, black anterior segment with white margin anteroventrally and posteroventrally. Anal fin creamy white with broad dark anteriorly tapering mid lateral stripe, becoming faint at anterior end. Caudal fin with broad rather dark transverse band distally and less dark band proximally, the two separated by a much narrower pale interspace. Lateral surface of

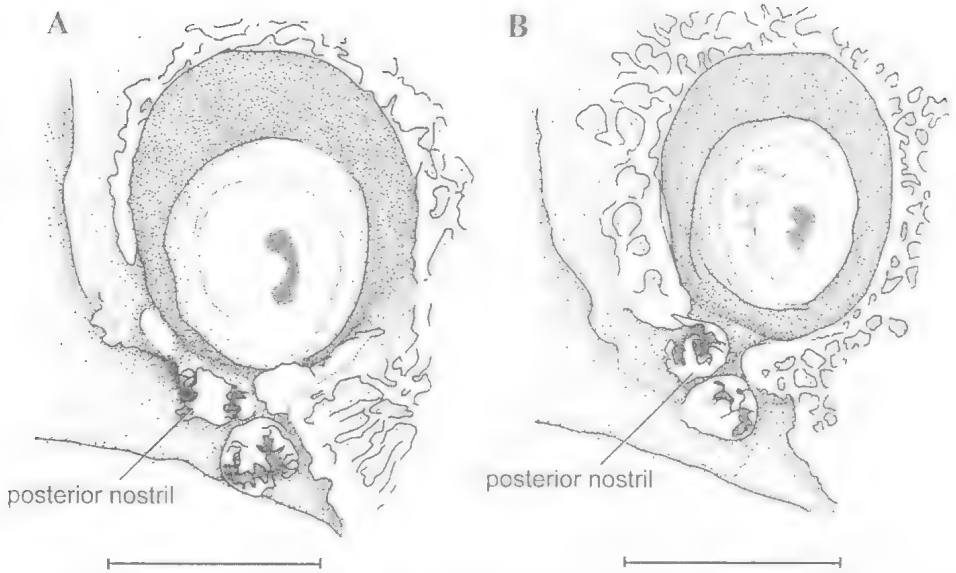



FIG. 4. Nostrils (left side) in A, *Ichthyscopus nigripinnis*, AMSI37479-001, 119mm SL, and C, *I. barbatus* NMVA13018, 130mm SL. Scale bars = 5mm.

pectoral fin with distinctly pale rays, charcoal intervening membranes and narrow pale distal margin; inner surface similar but with somewhat fainter pigmentation. Pelvic fins creamy white.

Juveniles (Fig. 7) pale below, dusky above, with narrow somewhat darker edged irregular pale longitudinal stripe immediately below lateral line under dorsal fin base and second broken stripe of similar breadth adjacent dorsal fin base; stripes breaking up and appearing as irregular blotches in larger juveniles; nape in small specimens with broad transverse pale saddle, lateral ends directed somewhat posteriorly, with margin irregularly defined by dark lines and spots; additional dark spots more or less in transverse rows anteriorly on fleshy part of nape and scattered in interorbital fossa; dorsal fin with black anterior segment as in adults and faint dusky markings posteriorly; caudal fin with broad dark distal band and faint dusky band more proximally, bands separated by a distinctly pale band with second pale band along proximal edge; pectoral fins mostly patterned as adults. Larger specimens pigmented like adults but often with two irregular narrow pale longitudinal markings on dorsal half of body variably on and posterior to posterior dark saddle and with two angled narrow pale marks on base of caudal fin.

Colour in life (270mm SL specimen), head pale tan-brown, freckled with cream spots; body slate grey with vague brownish reflections; caudal dusky, freckled white; anterior segment of dorsal fin with large vivid black spot.

DISTRIBUTION. Restricted to the coastal waters of northeastern Australia and southeastern Papua New Guinea from about the Laloki River, Papua New Guinea (9°13'S 146°55'E) to about Iluka, New South Wales (29°50'S 153°21'E) (Fig. 8A), at depths of 3-58m.

REMARKS. *Ichthyscopus nigripinnis* and *I. barbatus* are very similar, both in morphology and colour pattern. The 2 are most easily separated by the distinctive, partially differentiated, black anterior segment of the dorsal fin with 3 (rarely 4) spines in the former (mostly undeveloped with only 2 spines in the latter, Fig. 1), the shape of the posterior nostril (Fig. 4), the form of the margin of a skin flap on the lower jaw which adjoins the ventrolateral edge of the lower lip (Figs 3A,B), the nature of the crest of the fleshy horizontal subcleithral ridge and the absence in *I. nigripinnis* of chin barbels. Precise details of differences are presented in the diagnoses.

Morphologically, *I. nigripinnis* is most similar to *I. spinosus*, the 2 having the most distinctly differentiated anterior segment of the dorsal fin in the genus. The latter and other congeners differ from the new species most noticeably in having extremely different colour patterns. They are also distinguishable on the basis of various

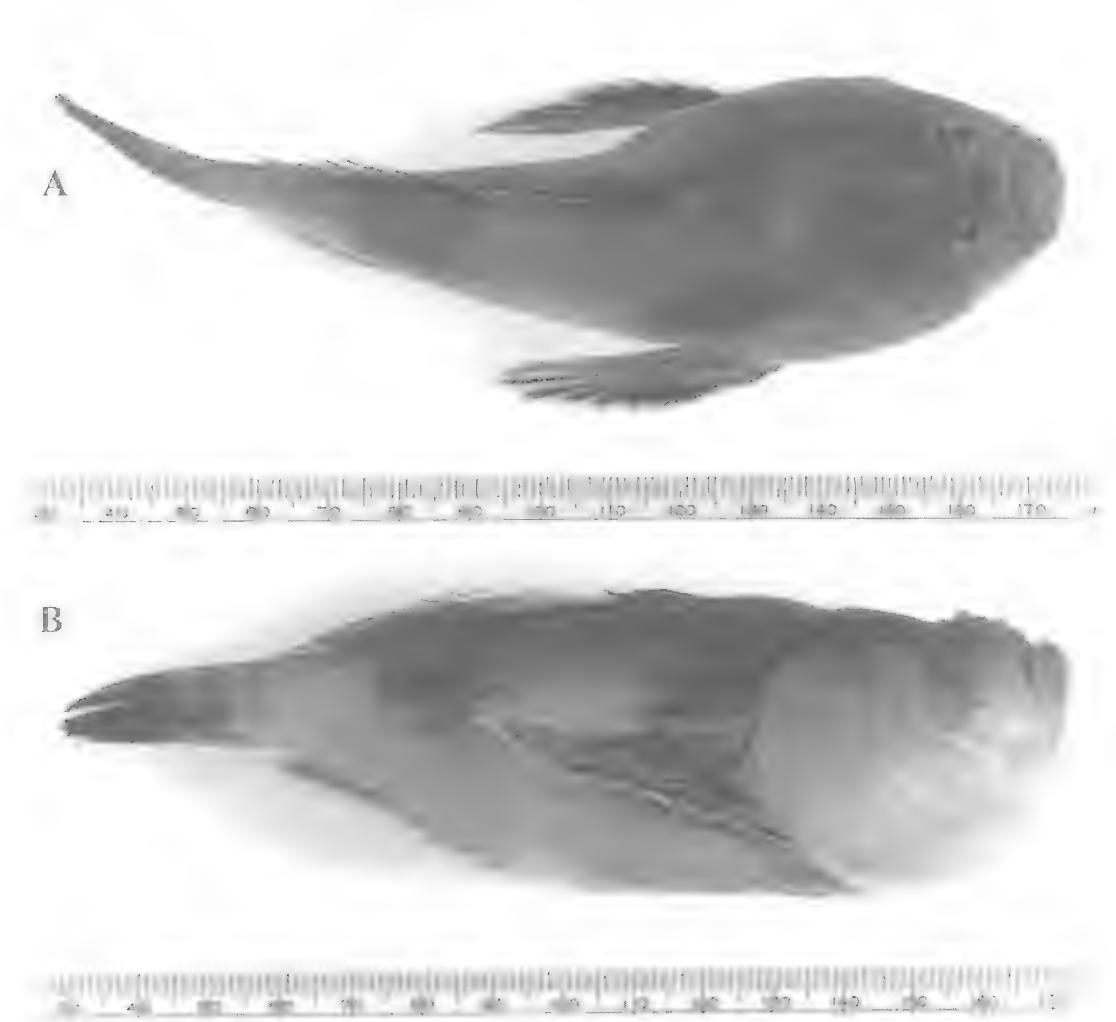



FIG. 5. *Ichthyscopus nigripinnis* sp. nov., holotype, QMI30217, 110mm SL A, dorsal and B, lateral views.

combinations of characters including the presence or absence of scales, number of vertebrae, the form of labial fimbriae, and both the extent and morphology of the cleithral flap and opposing horizontal fleshy subcleithral ridge.

**Ichthyscopus barbatus** Mees, 1960
(Figs 1B, 3B, 4B, 8A)

*Ichthyscopus barbatus* Mees, 1960: 49, figs 3, 4, 5a. Type locality – western coast of SW Australia between Rottnest I. and the Stragglers.

MATERIAL. New South Wales:- AMSIA245 (1, 142) off Norah Head, 33°17'S 151°37'E, 48-69m, 18 June 1921, F. McNeill & A. Livingstone; AMSI1875 (1, 227) off Port Jackson, 33°51'S 151°17'E, 128m, O. Meyer; AMSI3926 (1, 232) off Barrenjoey, 33°35'S 151°21'E, 51m, 1898; AMSI3927 (1, 198) off Broken Head, 33°27'S 151°34'E, 51m, 1898; AMSI18143-001 (1, 237) off Nelson Bay, 32°43'S 152°08'E, May 1974, Sydney Fish Markets; AMSI25863-001 (1, 187) south of Port Stephens, 32°49'S 152°02'E, 38-53m, 11 April 1985, FRV Kapala, K. Graham; AMSI34216-002 (1, 184) off Jervis Bay, 35°13'S 150°36'E, 23 February 1993, FRV Kapala, K. Graham; NMVA13018 (1, 130) Disaster Bay, 37°16.5'-37°16.8'S 149°59.1'-150°01.1'E, 24-33m, 11 August 1993, RV Southern Surveyor; South Australia:- SAM388 (1, 196) 33°46'S 133°30'E, 37m, 28 February 1981, T. Holder; SAM1065 (1, 130) 3 miles south of Evans I., 40m, 14 April 1982, K. & T. Olsen; SAM1111 (1, 143) 10.5-8.6 miles off Emu Bay, Kangaroo I., April-May 1981, I. Brown; SAM1204 (1, 118) 9.6 miles off Emu Bay, Kangaroo I., 31m, 27 January 1982, March & Bates; SAM1537 (1, 146) 5-5.5 miles off North Cape, Kangaroo I., 27-29m, 12 January 1982, I. Brown.

DIAGNOSIS. Dorsal fin with II spines and 17 or 17.5 soft rays, anterior end with low notch but not distinctly differentiated from rest of fin (Fig. 1B), 2nd fin ray element (= last spine) shortest,



FIG. 6. Dorsal surface of head in *Ichthyscopus nigripinnis*, paratype, QMI11908, 275mm SL, showing exposed bony surface.

elements becoming progressively longer posteriorly; posterior nostril circular (Fig. 4B); labial fimbriae simple, smooth-edged; skin flap on lower jaw adjacent to ventrolateral edge of lower lip with smooth margin (Fig. 3B), lacking fimbriae; each side of lower jaw with 2-9 teeth; chin with anteroposteriorly aligned pair of short barbels on symphysis; cleithral skin flap nearly twice length of cleithral spine; fleshy horizontal subcleithral ridge continuing on posterior side of pectoral fin axis to just below free posterior tip of cleithral skin flap, forming free pointed flap posteriorly; fleshy horizontal subcleithral ridge continuing on posterior side of pectoral fin axis only half way from base to tip of cleithral skin flap; crest of ridge fimbriate anterior and posterior to pectoral fin base; fimbriae on ridge anterior to pectoral fin base rather sparse, much simpler than fimbriae on opposing margin of cleithral flap, those posteriorly similar in structure to those of cleithral flap; scales present, in 28-45 oblique rows; sides with 2 broad dark saddles, positioned below anterior and posterior ends of dorsal fin; pectoral fin mostly dusky with pale distal margin and pale fleshy base.

DESCRIPTION. Dorsal fin rays II, 17 or 17.5; anal fin rays 16 or 16.5; caudal fin with 12 or 13 principal rays, 3-5 unsegmented procurrent rays dorsally and 1-4 unsegmented procurrent rays ventrally; pectoral fin rays 13-15 (usually 14); pelvic fin rays I, 5; vertebrae 9 + 17 or 18 (usually 9 + 17); epipleural ribs 8-11 (mean 9.50), situated on vertebra 4 or 5 - 11 to 14.

Body moderately deep, compressed posteriorly; head rather square in cross section (see Table 1 for morphometric data).

Head mostly encased in bone, without obvious joint lines dorsally; bony surface textured with fine low vermiculations; dorsal surface mostly flat, only slightly concave posterior to interorbital fossa. Interorbital fossa rectangular, width posteriorly slightly more than that between



FIG. 7. Juvenile *Ichthyscopus nigripinnis* sp. nov., paratype, NMVA20080, 54.8mm SL, lateral view.

orbits. Orbit circular, diameter distinctly greater than that of eye. Anterior nostril small, approximately 1/3 eye diameter, tubular, somewhat divided into two openings by midposterior thickening or T-shaped flap; anterior side with low rim providing notch, rim edged mostly with simple to broad lobate fimbriae. Opening of posterior nostril circular, anterior lobe tall, narrow, with numerous simple fimbriae, mesial and lateral flaps not especially prominent, each with fimbriate edges. Both lips with simple, smooth-edged fimbriae externally, fimbriae on lower lip occasionally branched at corner of mouth; 17-23 individual fimbriae on upper lip, 41-52 on lower; skin flap on lower jaw adjacent to ventrolateral edge of lower lip with smooth margin, lacking fimbriae; inner edge of upper and lower lips also with very fine, often distinctly subbranched to palmate fimbriate fringe. Upper jaw with band of numerous small slightly curved teeth; teeth not in distinct rows, about 2 or 3 teeth across band where broadest. Lower jaw in large specimens usually with about 6-9 widely spaced straight prominent narrow canines angled back into mouth on each side, posteriormost noticeably longer than others. Oral valve broad, fleshy, drawn upwards into a tri-peaked rectangular flap medially. Chin smooth, with anteroposteriorly aligned pair of short barbels on symphysis, posterior barbel longer. Dorsal half of opercular margin fimbriate, with 21-31 individual fimbriae; ventralmost simple, those dorsally with up to 8 simple lateral branches, branches rarely subdivided; opercular margin smooth ventrally.

Cleithral spine extending posteriorly almost to above dorsal extent of pectoral fin axis. Fleshy cleithral skin flap enveloping spine extending well past this point; underside of flap fimbriate with 21-28 individual fimbriae; fimbriae, including that at tip with up to 9 side branches on both anterior and posterior margins, those closest to tip with most branches, branches only occasionally subdivided into sub-branches (occurring most often proximally on flap); occasionally 1 or 2 simple fimbriae on dorsal edge of flap near tip. Narrow fleshy subcleithral ridge extending horizontally from opercular opening to dorsal extent of pectoral fin base, continuing on posterior side of pectoral fin axis only half way from base to tip of cleithral skin flap; crest of ridge fimbriate anterior and posterior to pectoral fin base; fimbriae on ridge anterior to pectoral fin base rather sparse, much simpler than fimbriae on opposing margin of cleithral flap, those posteriorly similar in structure to those of cleithral flap. No spines associated with subopercle, opercle, preopercle or basipterygium.

Dorsal fin rather long-based and low, anterior end with low notch but not distinctly separated into distinct anterior segment, 2nd fin ray element (= last spine) shortest, varying from considerably (almost half) to only slightly shorter than subsequent element, following elements becoming progressively longer posteriorly. Anal fin long-based and low. Caudal fin broadly rounded. Pectoral fin pointed, tip of 3rd ray at point, membrane incised slightly between tips. Pelvic fins strong and fleshy, inner 2 rays longest, interradial membranes more clearly incised in remaining rays. Ventral midline with medial ventral skin flap from anterior tip of basipterygium to center of pelvic fin base.

Scales prominent, cycloid, rectangular, arranged in 28-45 obliquely angled rows, with or without additional scales scattered at posterior end of caudal peduncle, up to 10 scales across patch in at least one specimen; underside of body naked anteroventral to an imaginary line connecting tip of cleithral skin flap and center of anal fin base. Lateral line pores in lines or clumps of 3-8 at dorsal end of each diagonal scale row. Nape between rows of lateral line pores devoid of scales; sensory pores virtually absent from nape except for those associated with lateral line.

Colour in alcohol brownish grey dorsally on sides and head, creamy white below with 2 pairs of broad dark saddles, 1 at origin of dorsal fin, extending onto cleithral flap ventrally; 2nd on and beneath posterior end of dorsal fin, extending well ventrally. Opercle, preopercle and much of maxilla creamy white; broad rectangular dark blotch on cheek; upper lip, lower lip and chin brownish grey; interorbital fossa rather dark. Dorsal fin dusky except for dark extensions of saddles onto fin and pale margin. Anal fin creamy white with faint dusky mid lateral stripe posteriorly (nearer distal margin than base). Caudal fin mostly dusky with narrow pale distal margin, broad transverse band proximally and dusky blotch dorsally on fleshy base. Lateral surface of pectoral fin mostly dusky with pale distal margin and pale fleshy base; inner surface pale. Pelvic fins creamy white. Juveniles unavailable.

Colour in life (see Gomon, 1994, fig. 631) pale brown above, white below, dorsal portion of head reddish brown, cheeks dark brown; 2 broad dark brown saddles on upper part of body below dorsal fin, first near origin and second near termination of fin; caudal fin dark brown; anal fin white with

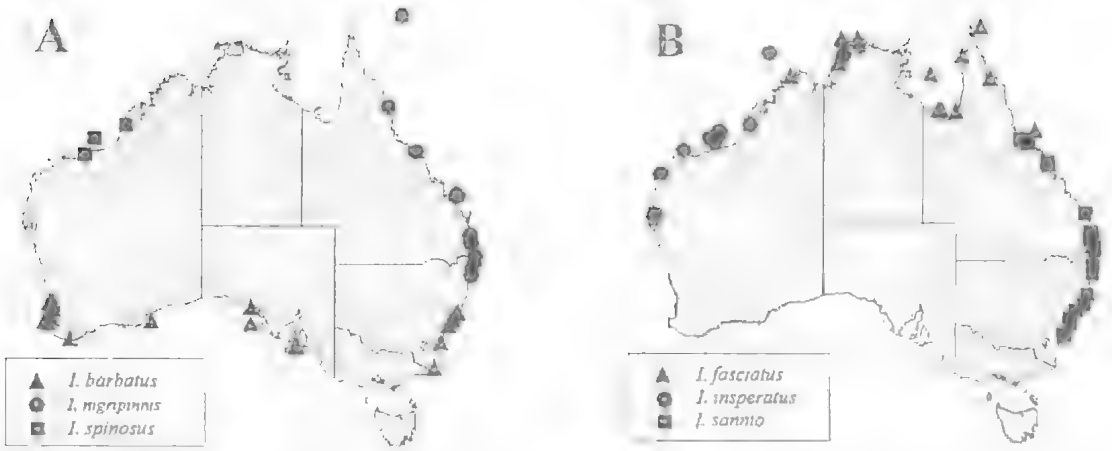



FIG. 8. Confirmed distributional records of A, *Ichthyscopus barbatus*, *I. nigripinnis* and *I. spinosus*, and B, *Ichthyscopus fasciatus*, *I. insperatus* and *I. sannio*.

narrow cream basal and subdistal stripes; pectoral fins medium brown with white margin; pelvic fin white.

DISTRIBUTION. Restricted to the coastal waters of southeastern and southwestern Australia between about Nelson Bay (32°43'S 152°08'E) and Disaster Bay (37°16.8'S 150°01.1'E) in NSW, and from Rottnest I., WA (31°59'S 115°45'E) to Kangaroo I., SA (35°36'S 137°31'E) (Fig. 8A), at depths of about 24-130m.

REMARKS. The gap in the known distribution of this species between southern NSW and Kangaroo I. does not appear to be an artefact of sampling. Specimens examined from SE and SW Australia do not possess any recognisable differences. Major water current patterns in the regions where the disjunct populations occur are presently such as to make it doubtful that the populations are still genetically linked by larval dispersal. It is more likely that the populations were contiguous until some time between the last extreme interglacial period (approximately 122,000BP) and the last sea level minimum (approximately 20,000BP; Frakes et al., 1992), and that genetic drift has not occurred to the extent that the 2 populations have noticeably differentiated. Comparisons of proteins between populations have not been undertaken as fresh material is not readily available

**Ichthyscopus fasciatus** Haysom, 1957
(Fig. 8B)

*Ichthyscopus fasciatus* Haysom, 1957: 139, fig. 1. Type locality – Cleveland Bay, near Townsville, N Qld.

MATERIAL. Queensland:- QMI10703 (1, 102, holotype) Cleveland Bay, 6 June 1955, G. Coates; QMI11203 (1, 111) SE corner of the Gulf of Carpentaria, CSIRO, ~1961; QMI23532 (1, 113) North of Cape Bowling Green, 19°17.4'S, 147°21'E, 18m, 12 November 1985, Queensland Department of Primary Industries, Fisheries; WAMP5139-001 (1, 243) no locality; Northern Territory:- NTMS10108-004 (1, 240) Port Essington, 11°16'S 132°09'E, 24m; NTMS11187-001 (1, 168) Fog Bay, 13°06'S 130°15'E; NTMS12434-029 (1, 111) Cobourg Peninsula, 11°06'S 132°06'E, 22m; NTMS12445-012 (1, 86.4) Cobourg Peninsula, 11°06'S 132°04'E, 20m; NTMS-12536-001 (1, 119) Cobourg Peninsula, 11°06'S 132°04'E, 20m; Western Australia:- WAMP28457-001 (1, 119) Admiralty Gulf, 14°20'S 125°53'E, 14.6-18.3m, 26 April 1968.

DIAGNOSIS. Dorsal fin with I spine and 17.5-20 soft rays, anterior end not partially differentiated into anterior segment, anteriormost fin ray element shortest, elements becoming progressively longer posteriorly; posterior nostril circular, positioned in anterior gap in bony orbit; labial fimbriae with lateral branches; skin flap adjacent to ventrolateral edge of lower lip with smooth margin; each side of lower jaw with 11-18 teeth; chin lacking barbels, but with bony ridge on either side; cleithral skin flap developed only as narrow margin along ventral edge of spine, barely extending posteriorly beyond tip; fleshy subcleithral ridge absent; scales present, in 52-84 oblique rows; sides with 5 or 6 broad dark bands dorsally, 2nd to 4th bands extending onto dorsal fin; pectoral fin pale, upper edge with broad wash of slightly dusky pigment laterally.

DESCRIPTION. Dorsal fin rays I, 17.5-20; anal fin rays 17-18.5; caudal fin with 12 principal rays

and 5 or 6 unsegmented procurrent rays dorsally and ventrally; pectoral fin rays 15-16; pelvic fin rays I, 5; vertebrae 9 + 18; epipleural ribs 8-10 (mean 9.11), situated on vertebra 4 or 5 -12 to 14.

Body moderately slender, compressed posteriorly; head rather square in cross section (see Table 1 for morphometric data).

Head mostly encased in bone, without obvious joint lines dorsally; bony surface textured with moderately rugose low irregular vermiculations; dorsal surface mostly flat, only slightly concave posterior to interorbital fossa; bony rim of orbits slightly raised posteromesially. Interorbital fossa rounded posteriorly, space somewhat constricted between eyes in small specimens, width posteriorly about 1.5 times that between eyes. Orbit circular, diameter distinctly greater than that of eye. Anterior nostril small, approximately 1/4 eye diameter, distinctly tubular, rim edged with simple fimbriae, single large bilobate flap midposteriorly, flap fimbriate in large specimens. Opening of posterior nostril circular, situated in anterior gap in bony orbit; nostril with anterior flap and smaller medial flap, each with fimbriate edges. Both lips fimbriate externally, fimbriae with 1 or 2 rows of up to 15 short, simple, evenly-spaced, lateral branches on either side, those in lower jaw better developed than in upper, branches occasionally bifurcate on fimbriae near symphysis of jaw, outer 3-5 fimbriae in lower jaw simple; 23-26 individual fimbriae on upper lip, 38-45 on lower; skin flap on lower jaw adjacent to ventrolateral edge of lower lip with smooth edge; inner edge of upper and lower lips also with fimbriate fringe, those in upper mostly simple, palmate in lower. Upper jaw with band of numerous small slightly curved teeth; teeth not in distinct rows, about 3 teeth across band where broadest. Lower jaw in large specimens with about 17 or 18 narrowly spaced short canines angled back into mouth on each side. Oral valve narrow with smoothly curved margin. Chin often with prominent lateral bony ridge on either side, ridge with extremely rugose to smooth surface (obscured by skin in some); symphysis smooth, without barbels; some with bony rugose patch laterally on expanded posterior end of maxilla and just below on lower jaw. Dorsal half of opercular margin fimbriate, with 11-18 individual fimbriae; most fimbriae simple, those dorsally with up to 5 irregular lateral branches; opercular margin smooth ventrally.

Cleithral spine extremely broad basally, with rugose lateral surface covered by skin, extending posteriorly almost to above dorsal extent of pectoral fin axis. Fleshy cleithral skin flap developed only as narrow margin along ventral edge of spine, barely extending posteriorly beyond tip; underside of flap edged with 8-14 mostly simple fimbriae. No narrow fleshy subcleithral ridge on pectoral fin base below cleithral flap. Upper half of opercle and preopercle with minute surface rugosity, similar in form but finer in texture than dorsal and cranial plates, lower halves with simple fine striae radiating ventrally. No spines associated with subopercle, opercle, preopercle or basipterygium.

Dorsal fin rather long-based and low, anterior end not separated into anterior segment; elements at anterior end of fin becoming progressively longer. Anal fin long-based and low. Caudal fin mostly truncate, only slightly rounded. Pectoral fin pointed, tip of 5th ray at point, membrane incised slightly between tips. Pelvic fins strong and fleshy, inner two rays longest, interradial membranes more clearly incised in remaining rays. Ventral midline with medial ventral skin flap from anterior tip of basipterygium to center of pelvic fin base.

Scales distinct, cycloid, rectangular, rather small, more or less arranged in 52-84 obliquely angled rows, in some specimens scales absent from anteriormost portion of sides (naked area reaching posteriorly to about center of pectoral fin in one specimen), rows angled obliquely forward from upper portion of sides in some, scales on caudal peduncle more perch-like in arrangement in some specimens; underside of body naked anteroventral to an imaginary line connecting tip of cleithral skin flap and center of anal fin base. Lateral line pores singular, each at posteroventral end of embedded tube. Nape between lateral lines devoid of scales; sensory pores virtually absent from nape except for those associated with lateral line.

Colour in alcohol whitish with 5 evenly spaced broad brown bands on dorsal third of sides, bands fading midlaterally, first crossing nape above cleithral spine and last positioned across caudal peduncle adjacent to proximal ends of caudal fin rays; upper surface of head and chin paler brown; slightly darker edged pale spot in interorbital fossa between anterior edges of eyes and two smaller spots of similar pigmentation on chin. Second band extending onto and covering anterior end of dorsal fin, 3rd and 4th bands also extending onto dorsal but not quite reaching distal edge; remainder of dorsal, as well as

caudal, anal, pectoral and pelvic fins pale; upper edge of pectoral fin with broad wash of slightly dusky pigment laterally. Juveniles as described for adults.

Colour in life (after Sainsbury et al., 1984, p. 267; Gloerfelt-Tarp & Kailola, 1984, p. 244; Allen & Swainston, 1988, fig. 819) fawn above, white below, with 5 or 6 dark brown bands across back to mid-sides, bands fading to indefinite yellow bands on ventral surface; nape brown. Haysom (1957) reported 'head is crossed by three irregular brown bands — the first, which is ill-defined across the snout, the 2nd just behind the eyes, and the 3rd, which is almost as dark as the body bands, across the occipital region' and Kailola (1975) described the interorbital fossa and chin as having 'oval, brown-edged white ocelli'); cleithral spine and fleshy ventral flap dark brown with yellow fringe; dorsal fin with dark brown extension of body bands and yellow margin; caudal, pectoral and pelvic fins bright orange or yellow with white bases and margins; pectoral with brown smudge centrally; anal fin white.

DISTRIBUTION. Restricted to the coastal waters of northern Australia and southern New Guinea between the Admiralty Gulf, WA (14°10'S 126°00'E) and Port Essington, NT (11°16'S 132°09'E) north to southern Irian Jaya (= south coast of Dutch New Guinea; Mees in Kailola, 1975) in the west and from the central portion of the Gulf of Carpentaria (14°00'S 138°36'E) through the Torres Strait (Coconut I., 10°03'S 143°06'E; Kailola, 1975) to Cape Bowling Green, Qld (19°17'S 147°21'E) in the east (Fig. 8B), at depths of about 9-24m.

REMARKS. *Ichthyscopus fasciatus* is the most distinctive species of the genus, having easily the least modified suite of characters. The fleshy skin flap associated with the cleithral spine is entirely confined to the ventral margin of the spine, barely extending posteriorly beyond its tip. The horizontal fleshy ridge on the base of the pectoral fin of its congeners is absent in *I. fasciatus* and fimbriae associated with the operculum and cleithral flap are the least developed of the species. Teeth of the lower jaw in this species are more similar to those of other uranoscopid genera, like *Uranoscopus* (Pietsch, 1989), in being rather short and numerous. This more than likely represents a primitive condition for the genus.

## **Ichthyscopus insperatus** Mees, 1960
(Figs 3C, 8B)

*Ichthyscopus insperatus* Mees, 1960: 54, figs 8, 9. Type locality – Roebuck Bay, NW Australia.

MATERIAL. Western Australia:- NMVA1909 (1, 116) North of Red Point, 18°42'-18°40'S, 119°37'-119°41'E, 114m, 12 March 1981, RV Hai Kung; WAMP4962-001 (1, 107) Shark Bay, 10 October 1960, R.J. McKay; WAMP8158-001 (1, 115) Shark Bay, 1964, Poole Brothers, 'Bluefin'; WAMP11839-001 (1, 33.0) Shark Bay, 19 October 1964, E. Barker; WAMP14808-001 (1, 177) Shark Bay, March 1965, A. McKenzie; WAMP27241-002 (1, 91.7) 18°44'S 119°26'E, 12 March 1981, N. Sinclair, 'Hai Kung'.

DIAGNOSIS. Dorsal fin with I spine and 18 or 19 soft rays, anterior end not differentiated into anterior segment, anteriormost fin ray element shortest, elements becoming progressively longer posteriorly; posterior nostril elongate, rimming fleshy anterior gap in bony orbit; labial fimbriae usually with numerous (up to 13) short tuberculate lateral branches; skin flap adjacent to ventrolateral edge of lower lip with smooth margin, usually with broad tab-like bulge on outer surface (Fig. 3C); each side of lower jaw with 9-14 teeth; chin without barbels; cleithral flap length twice that of spine; subcleithral ridge extending to about midpoint between tip of cleithral spine and tip of cleithral skin flap, forming free pointed flap posteriorly; crest of ridge with or without low mound-like flaps anterior to pectoral fin base, irregular posterior to it with fimbriate posterior tip, sometimes having fine irregular fimbriae on flaps in large specimens; scales absent; sides pale with 5 broad saddles on dorsal half of sides, saddles in smaller specimens in form of dark-edged 'halos', larger specimens with dark 'halos' less intense but with darker inner and outer edges, and ventral parts becoming faint leaving an impression of 9 or 10 dark edged vertical bands; pectoral fins pale with dusky hue centrally and somewhat posteriorly.

DESCRIPTION. Dorsal fin rays I, 18 or 19; anal fin rays 16 or 17; caudal fin with 12 principal rays, 3 or 4 unsegmented procurrent rays dorsally and 1-3 unsegmented procurrent rays ventrally; pectoral fin rays 14 or 15; pelvic fin rays I, 5; vertebrae 9 + 17 (rarely 9 + 16); epipleural ribs 8 or 9 (mean 8.40), situated on vertebra 4 or 5 – 11 or 12.

Body moderately deep, compressed posteriorly; head rather circular in cross section (see Table 1 for morphometric data).

Head mostly encased in bone, without obvious joint lines dorsally; bony surface textured with fine low vermiculations; surface visibly concave posterior to interorbital fossa. Interorbital fossa rectangular, width posteriorly only slightly more than that between orbits. Orbit somewhat rectangular, diameter distinctly greater than that of eye. Anterior nostril small, approximately 1/3 eye diameter, tubular, divided into 2 openings by T-shaped midposterior flap; anterior side with low rim providing notch, rim and posterior flap edged with simple to arborescent fimbriae. Opening of posterior nostril elongate, rimming fleshy anterior gap in bony orbit; low anterior, lateral and mesial flaps with arborescent fimbriae, posterior rim smooth; nostril not noticeably subdivided. Lips with numerous fimbriae externally, some with many (up to 13) short tuberculate branches on each side, those toward corners of mouth with shortest branches or without branches; 19 or 20 (34 in 1 specimen) individual fimbriae on upper lip, only 1 or 2 at each corner smooth-edged, 44-49 on lower with 11 or 12 at each corner smooth-edged; skin flap on lower jaw adjacent to ventrolateral edge of lower lip with smooth edge, usually with broad tab-like bulge on outer surface; inner edge of upper and lower lips also with fimbriate fringe, fimbriae only occasionally branched. Upper jaw with narrow band of numerous small slightly curved teeth; teeth not in distinct rows, about 2 or 3 teeth across band where broadest. Lower jaw in large specimens with 9-14 straight rather short but prominent narrow canines angled back into mouth on each side, 1 or 2 occasionally in a second row, posteriormost slightly longer than others. Oral valve broad, fleshy, drawn upwards into a low point medially. Chin smooth, without barbels. Dorsal half of opercular margin fimbriate, with 15-26 individual fimbriae; fimbriae branched except several simple at dorsal and ventral extremes, up to 4 or 5 lateral branches, some divided to base, best developed in large specimens; opercular margin smooth ventrally.

Cleithral spine extending posteriorly to above dorsal extent of pectoral fin axis. Fleshy cleithral skin flap enveloping spine, length of flap twice that of spine; underside of flap fimbriate with about 15-21 individual fimbriae; fimbriae often broad, with up to 4 or 5 side branches on both anterior and posterior margins including that at tip of flap, those closest to tip with most branches, branches only occasionally subdivided into sub-branches (occurring most often proximally on flap); up to 9 tuberculate fimbriae on dorsal edge of flap near tip. Narrow fleshy subcleithral ridge extending horizontally from opercular opening to dorsal extent of pectoral fin base, continuing on posterior side of pectoral fin axis about half way from tip of cleithral spine to tip of cleithral skin flap, forming free pointed flap posteriorly; crest of ridge irregular, with or without low mound-like flaps anterior to pectoral fin base and occasionally with flaps posterior to it, only posterior tip fimbriate in small specimens, mounds and flaps with fine irregular fimbriae in large specimens. No spines associated with subopercle, opercle, preopercle or basipterygium.

Dorsal fin rather long-based and low, anterior end not separated into anterior segment; rays progressively longer at anterior end of fin. Anal fin long-based and low. Caudal fin mostly truncate, only slightly rounded. Pectoral fin pointed, tip of 5th ray at point, membrane incised slightly between tips. Pelvic fins strong and fleshy, inner 2 rays longest, interradial membranes more clearly incised in remaining rays. Ventral midline with medial ventral skin flap from anterior tip of basipterygium to rear of pelvic fin base.

Scales apparently absent, although some faint skin folds reminiscent of diagonal scale rows sometimes visible. Lateral line pores in diagonal rows with 3-8 pores per row. Sensory pores otherwise absent from nape but obviously present posteriorly on bony head shield.

Colour in alcohol predominantly pale, slightly duskier dorsally with 5 broad saddles on dorsal half of sides, saddles in smaller specimens in form of dark-edged 'halos', centers having same pale hue as elsewhere; larger specimens with dark 'halos' less intense but with darker inner and outer edges, and ventral parts becoming faint leaving the impression of 9 or 10 dark edged vertical bands; first 2 'halos' continuous across nape and back, last 3 extending onto base of dorsal fin, viewed as complete ovals from side. Head slightly dusky dorsally with faint small darker marks in transverse row just behind posterior edge of interorbital fossa, and ocellated dusky reticulations on lips and anterior portion of membranous interorbital fossa. Dorsal fin pale with dark extensions of dark 'halos' and dark blotches marginally above and before 'halos' on body. Anal fin pale. Caudal fin pale with 2 broad dark bands, 1 a third of the way from base to tip and 2nd submarginally. Pectoral fins pale with dusky hue centrally and somewhat posteriorly. Pelvic fins pale. Juveniles pigmented as adults except dorsal surface of bony shield posterior to

eyes with 3 close set transverse bands, pigmented like, but much narrower than saddles on sides.

Colour in life (after Sainsbury et al., 1984, p. 267; Gloerfelt-Tarp & Kailola, 1984, p. 244; Allen & Swainston, 1988, fig. 820) grey-olive above, head with orange tints, white below; 10-12 dark brown narrow double cross-bands over back to mid-sides. Dorsal fin white with 3 or 4 broad oblique charcoal bands; anal and ventral fins white with yellow tints; caudal fin white with 2 or 3 crescentic charcoal bands; pectoral fin dusky with broad yellow margin.

DISTRIBUTION. Restricted to the coastal waters of northwestern Australia from about Shark Bay, WA (25°21'S 113°44'E) to about Darwin, NT (12°27'S 130°48'E) (Fig. 8B), at depths of 76-114m.

REMARKS. Scale development of most species in this genus is extremely variable with examples frequently having scale rows angled in the 'opposite' direction, scales scattered in a non-uniform fashion, especially on the caudal peduncle, or reduced to an imbricate condition resembling that of most perch-like fishes. The absence of scales in this species is merely an extreme example of the varying degrees of scale reduction seen in species like *I. fasciatus*, and does not warrant generic separation.

### **Ichthyscopus sannio** Whitley, 1936
### (Fig. 8B)

*Ichthyscopus sannio* Whitley, 1936: 45. Type locality Patonga, Broken Bay, NSW.

MATERIAL EXAMINED. Queensland:- AMSI426 (1, 76+); AMSI12550 (1, 142) Moreton Bay; AMSI16796-001 (1, 259) Fan Beach, Mackay, 21°09'S 149°12'E, 29 December 1972, J. Davies; AMSI21149-002 (1, 45) Bohle R. estuary, 19°12'S 146°42'E, 8 October 1965, F. Talbot & party; AMSI22769-008 (1, 96) Sarina Beach, north end, 21°24'S 149°19'E, 1-2m, 17 June 1980, G., M. & M. Hardy; AMSI22774-010 (2, 131-137) Alva Beach near Ayr, 19°27'S 147°29'E, 1-2m, 21 June 1980, G., M. & M. Hardy; AMSI23319-041 (1, 21) at mouth of Mangrove Ck E of Townsville, 19°16'S 147°03'E, 2m, 29 October 1982, D. Heese, D. Rennis; AMSI25687-001 (1, 168) Jumpin Pin, Stradbroke I., 27°44'S 153°26'E, 8 October 1984, C. Keenan; QMI1657 (1, 233) Moreton Bay, 27 January 1914, Campbell & Wickworth; QMI2196 (1, 95) Sandgate, Moreton Bay, 27°19'S 153°04'E, 5 October 1914, T.W. Grice; QMI4972 (1, 82) Sandgate, Moreton Bay, 27°19'S 153°04'E, 13 August 1932, R. Marchant, QMI5239 (1, 319) Mooloolaba, 26°41'S 153°07'E, 8 May 1935, Anderson; QMI6951 (1, 354) Surfers Paradise, 28°00'S 153°26'E, 24 June 1940, J. Thomson; QMI7026 (1, 385) Jumpin Pin, Stradbroke I., 27°44'S 153°26'E, 28 October 1940, C.E. Gilbert; QMI7719 (1, 276) Jumpin Pin, Stradbroke I., 27°44'S 153°26'E, 30 May 1947, A. Leonard; QMI7937 (1, 226) Tallebudgera Ck, 28°07'S 153°27'E, 26 February 1953, J. Bolton; QMI7995 (1, 196) Burleigh Hds, 28°05'S 153°27'E, 6 March 1955, J.B. Woodland; QMI8007 (1, 195) Burrum Hds, 25°11'S 152°37'E, 31 August 1955, A.E. Drimmer; QMI8229 (1, 191) Wilston Ck, Brisbane, 27°27'S 153°01'E, 4 September 1961, R. Ebrington; QMI8307 (1, 230) Tingalpa Ck mouth, Moreton Bay, 27°29'S 153°11'E, 16 June 1964, T.A. Strelow; QMI8308 (1, 231) off Birkdale, Moreton Bay, 27°29'S 153°13'E, 28 June 1964, J. Brooks; QMI9860 (1, 181) Coochin Ck mouth, Pumicestone Passage, 26°55'S 153°04'E, 5 January 1970, L. Glover; QMI11837 (1, 94) Bulwer, Moreton Bay, 27°05'S 153°22'E, 1950, K.E. Rowell; QMI12040 (1, 288) Lake Coombabah mouth, 27°55'S 153°21'E, 25 September 1951, E. Malmberg; QMI20958 (1, 431) Caloundra bar, 26°49'S 153°08'E, 1 May 1984, Redcliffe Trawler Seafoods; QMI26357 (1, 64) Caboolture R. mouth, 27°09'S 153°02'E, 5 November 1974, H. Weng; New South Wales:- AMSIA3567 (1, 235) Ballina, 28°52'S 153°34'E; AMSIA6309 (1, 210, holotype) Broken Bay, Patonga, 33°33'S 151°16'E; AMSIA6538 (1, 223) Nowra, Greenwell Point, 34°53'S 150°39'E, 9 December 1935, F. Rodway; AMSIB1363 (1, 151) Laurieton, 31°39'S 152°48'E, 1944; AMSIB2152 (1, 330) Nambucca Hds, 30°39'S 153°00'E, 1948; AMSIB2593 (1, 224) Laurieton, 31°39'S 152°48'E, 1950; AMSIB2794 (1, 108) South-West Rocks, 30°53'S 153°02'E; AMSIB3911 (1, 275) Sydney, Coal and Candle Ck, 33°38'S 151°13'E, 1958; AMSIB5072 (1, 208) Lake Macquarie, 32°59'S 151°35'E; AMSIB5085 (1, 164) Myall Lakes, Buladelah, 32°26'S 152°24'E; AMSIB5689 (1, 134) Ettalong Beach, 33°31'S 151°19'E, 1962; AMSIB6319 (1, 212) Kempsey District, Hat Head, 31°04'S 153°03'E; AMSIB6393 (1, 178) Botany Bay, Dolls Point, 34°00'S 151°08'E, 1963; AMSIB7787 (1, 150) Hawkesbury R., 33°35'S 151°10'E, 1967; AMSI2999 (1, 70,6) Newcastle, 32°56'S 151°46'E; AMSI5965 (1, 305) no locality, March 1903, J. Chimiery; AMSI7889 (1, 61.2) Lane Cove R., 33°47'S 151°08'E; AMSII3019 (1, 261) no locality, 5 March 1912, State Fisheries; AMSII5019 (1, 232) no locality, D. Stead; AMSII5020 (1, 230) no locality, D. Stead; AMSII5323-003 (1, 358) Smiths Lake, W of Horse Point, 32°19'S 152°28'E, 3m, 1968; AMSII5672-001 (1,219) Forster, Wallis Lake, 32°12'S 152°30'E, 1970; AMSII5749-001 (1, 247) Kiteare, 33°32'S 151°22'E, 5m, 1970; AMSII6847-021 (1, 21.3) ACT, Jervis Bay, Greenpatch Beach, 150°44'E 35°08'S, 1m, 24 June 1971, D. Pollard & P. Straw; AMSII9340-001 (1, 51.2) Clarence R., Palmers I., 29°27'S 153°17'E, 1975; AMSII9947-001 (1, 205) Hawkesbury R., Jerusalem Bay, 33°38'S 151°10'E, 5m, 1974; AMSII9948-009 (1, 32.2) Hawkesbury R., Jerusalem Bay, 33°38'S 151°10'E, 2m, 1974.

DIAGNOSIS. Dorsal fin with II or III spines and 16-17.5 soft rays, first 2 spines close together, often with tips projecting, 3rd spine much shorter, difficult to distinguish from enveloping skin or absent, a shallow concavity preceding soft rays only partially differentiating anterior part of dorsal fin into a short anterior segment (Fig. 11B); posterior nostril oval to circular, situated in

anterior gap in bony orbit; labial fimbriae with numerous short subdivided lateral branches (up to 16) on each side, branches longer distally; skin flap adjacent to lower lip smooth to distinctly crenulate; lower jaw with 12-21 teeth on each side; chin without barbels; cleithral skin flap slightly less than twice length of cleithral spine; fleshy horizontal subcleithral ridge continuing on posterior side of pectoral fin axis to just beyond half distance from tip of cleithral spine to posterior end of cleithral skin flap, forming a short free tip posteriorly; crest of subcleithral ridge discontinuous on opposing sides of pectoral fin axis, fimbriate along its length, fimbriae short, simple and closely spaced; scales present, in 47-59 oblique rows; a low blade-like skin flap along ventral midline from anus to midbase of pelvic fins; upper body with 2 poorly defined broad dark brown saddles positioned below dorsal fin anteriorly and posteriorly and with numerous irregular large white spots and blotches; nape and upper part of head with many small creamy-white spots.

DESCRIPTION. Dorsal fin rays II or III, 16-17.5 (usually III, 16.5), last element often small and very close to penultimate ray; anal fin rays 16.5-17.5 (usually 17.5), last element as in dorsal fin; caudal fin with 12 or 13 principal rays and 3-5 unsegmented procurrent rays dorsally and ventrally; pectoral fin rays 17 or 18 (usually 17); pelvic fin rays I, 5; vertebrae 9 + 18; epipleural ribs 7-9 (mean 8.08), situated on vertebra 4 or 5-11 or 12.

Body moderately deep, compressed posteriorly, head rather square in cross section (see Table 1 for morphometric data).

Head mostly encased in bone, without obvious joint lines dorsally; bony surface textured with fine low vermiculations; dorsal surface mostly flat, only slightly concave posterior to interorbital fossa. Interorbital fossa rounded posteriorly, width posteriorly slightly less than that between orbits. Orbit circular, diameter distinctly greater than that of eye. Anterior nostril small, approximately 1/3 eye diameter, tubular, rim edged by fimbriae with numerous branches, those anteriorly and posteriorly in clumps and somewhat thickened, those laterally slightly smaller and more flap-like. In juveniles, anterior nostril with fimbriae much less branched and midposterior flap prominent, extending forward to meet thickened inner edge of anterior fimbriae. Opening of posterior nostril oval to circular, situated in anterior gap in bony orbit; nostril anteromesially with 2 prominent thickened fimbriate flaps and usually several smaller branched fimbriae; nostril posterolaterally with low rim at fleshy margin of orbit, fimbriae here short, sparse and mostly simple, larger specimens with fine papillae inside nostril on inner margin. Both lips with numerous brush-like fimbriae externally in adults, fimbriae simple in juveniles; adult fimbriae with up to 16 rows of evenly spaced lateral branches on each side, each branch with up to 5 short tuberculate sub-branches; fimbriae occasionally bifurcate near symphysis of jaw; internally (beneath distal tip) all but outer 5-7 rows of fimbriae of upper jaw with a simple barbel, varying from short, tuberculate and poorly developed laterally, to elongate mesially; fimbriae of lower jaw with 1-3 simple to feebly branched elongate barbels internally on all but outer 8-15 fimbriae, those laterally shorter but thin and well developed; 27-36 individual fimbriae on upper lip, 41-51 on lower lip; skin flap on lower jaw adjacent to ventrolateral edge of lower lip with smooth to weakly crenulate margin in juveniles and small adults becoming distinctly crenulate medially in large specimens. Upper jaw with broad band of numerous small slightly curved teeth; teeth not in distinct rows, about 4 or 5 teeth across band where broadest. Lower jaw with 12-21 teeth on each side, including a group of small to minute teeth anteriorly (most clustered near symphysis), about 8-10 straight prominent canines angled back into mouth on each side, posteriormost canines noticeably larger, more broadly-based and strongly angled posteriorly. Oral valve broad, fleshy, drawn upwards into a low point medially. Chin smooth, without barbels. Dorsal half of opercular membrane fimbriate, with 12-19 individual fimbriae; ventralmost poorly developed and simple, those above flap-like with up to 10 variably arborescent branches; opercular margin smooth ventrally.

Cleithral spine extending posteriorly to or just beyond dorsal extent of pectoral fin axis. Fleshy cleithral skin flap enveloping spine extending well past this point, somewhat less than twice length of cleithral spine; underside of flap fimbriate with 15-22 individual fimbriae; fimbriae, including that at tip of flap with up to 12 subdivided arborescent branches on both anterior and posterior margins, dorsal edge of flap near tip smooth in juveniles but with up to about 12 small pointed feebly branched to simple brush-like fimbriae in large specimens. Narrow fleshy subcleithral ridge extending horizontally from

opercular opening to dorsal extent of pectoral fin base, continuing on posterior side of pectoral fin axis to just beyond midpoint between tip of cleithral spine and tip of outstretched cleithral skin flap, forming a short, free, pointed to fimbriate tip posteriorly; crest of ridge discontinuous at and just anterior to pectoral fin axis, fimbriate along most of its length, fimbriae short, simple and closely spaced, usually rather sparse anterior to pectoral fin base. No spines associated with subopercle, opercle, preopercle or basipterygium.

Dorsal fin rather long-based and low, anterior end partially separated into short anterior segment by shallow notch, first 3-4 elements relatively short, embedded in thick skin in large specimens, 3rd shortest, 4th longer than preceding elements; subsequent rays becoming progressively longer. Anal fin long-based and low. Caudal fin truncate to slightly rounded with branched tips of caudal rays extending slightly beyond membrane. Pectoral fin pointed, tip of 5th ray at point, membrane incised slightly between tips. Pelvic fins strong and fleshy, innermost ray longest, interradial membranes most clearly incised between first 4 rays. Ventral midline with prominent medial skin flap from anterior tip of basipterygium to rear of pelvic fin base, flap continuing posteriorly to anus, firstly as an inconspicuous low ridge but gradually deepening to form a thin blade-like flap.

Scales prominent, cycloid, rectangular, arranged in 47-59 (usually 50-52) obliquely angled rows (including smaller scales in less well defined rows on upper corner of caudal peduncle), occasionally two scale rows merging into one as they proceed ventrally; 8 of 25 specimens with patches of scale rows (usually below rear of soft dorsal or on caudal peduncle) directed dorsoposteriorly on one or both sides instead of typical ventroposterior pattern; additional small scales medially on upper half of caudal base (up to about 7 rows horizontally); peduncular scale rows from posterior end of anal fin base to distal corner of peduncle 16-20 (usually 17 or 18). Underside of body naked anteroventral to an imaginary line connecting terminal skin flap of subcleithral ridge to anterior 1/4 to 1/3 of anal fin base. Lateral line pores in angled lines or clumps of 1-4 at dorsal end of each diagonal scale row. Nape between lateral lines devoid of scales; sensory pores virtually absent from nape except for those associated with lateral line. Three to 4 smooth irregular-oval platelets, perforated by numerous pores, on upper 2/3 of caudal base immediately posterior to lateral scale rows, lower platelet largest.

Colour in alcohol dusky to dark brown on upper half of head and body, with irregular large pale spots and blotches, some with dark centers; an elongate pale blotch or stripe laterally below posterior end of dorsal fin extending to caudal base; 2 poorly defined dark saddles on sides (conspicuous in juveniles), first extending from origin of dorsal fin to about 4th dorsal fin element, 2nd at rear of dorsal fin base terminating at penultimate dorsal ray, both saddles reaching vertically to just below lateral midline of body. Nape, anterior half of cleithral skin flap, top of head, cheeks, lips and chin with numerous small close-set pale spots (less conspicuous on bony head shield), those anteriorly on head smallest; numerous small dark or dusky dots also scattered over this area. Cheek with large dark brown triangular blotch, distinct in juveniles, somewhat diffuse in larger specimens. Lower body and head including operculum pale. Dorsal fin dark with pale variegations forming irregular transverse bands, first 2-3 dorsal fin elements dusky to black, often with a pale spot at base of 1st spine and adjacent interspinous membrane. Anal fin pale, juveniles with diffuse dusky basal stripe on posterior half of fin and body adjacent to fin. Caudal fin pale to dusky with most of upper and lower margins and tips of rays distinctly pale; occasionally pale blotches or longitudinal bars centrally or posteriorly on fin. Pectoral fin uniformly pale basally; rays usually dark, occasionally pale, peppered with dusky melanophores; posterodorsal and ventral margins of fin pale, margins broad in juveniles. Pelvic fins pale, often with dusky melanophores on rays and a dusky tip posteromesially, the latter most prominent in juveniles.

Colour in life (see Grant, 1987, fig. 694a, 694b) as above, pale spots and blotches vivid to creamy white, dusky to dark areas brownish; lower portions of head, body and fins creamy white; operculum creamy white with flesh-pink tint; upper portion of body dark olive brown to light tan; saddles and triangular blotch on cheeks dark brown to dusky charcoal; caudal and margin of pectorals cream to yellow.

DISTRIBUTION. Restricted to the central coastal waters of E Australia between about Bohle River, Townsville, Qld (19°12'S 146°42'E) and Jervis Bay, NSW (35°08'S 150°44'E) (Fig. 8B), at depths of less than 10m.

REMARKS. Mees (1960) considered the Australian population described by Whitley (1936) as *I. sannio* to represent a subspecies of *I. lebeck* (Bloch & Schneider, 1801), the type of the latter from Tranquebar, India. He regarded the structure of the posterior nostril, the only feature in which he was able to discern differences in the 2 populations, not to be sufficiently significant as to warrant the recognition of the 2 as more than 'geographical races' (= subspecies). As specimens from China and Japan share a circular posterior nostril, Mees judged the northwestern and southwestern Pacific populations to be con-subspecific. We consider the 3 populations to be separate species, a notion supported by Kishimoto (pers. comm.) who has examined the taxa in greater detail. Mees provided a thorough synonomy for the Australian *I. sannio*.

*Ichthyscopus sannio* is separable from both the Indian Ocean and NW Pacific species in having 2 poorly defined broad dark brown saddles across the upper body (absent in northern hemisphere species), a distinguishable notch defining a somewhat separate anterior dorsal fin that is noticeably darker than the fin posteriorly in adults (not distinctively darker in the northern hemisphere species), and a smooth edge, rather than crenulations or tab-like cirri on the ventral opercular margin anterior to the pelvic fin bases. The Indian Ocean *I. lebeck* is distinctive within the genus in having the posterior nostril produced posteromesially in the infraorbital space along the bony rim defining the mesial side of the orbit. The nostril reaches posteriorly to a point in line with the posterior margins of the orbits. In other species of *Ichthyscopus*, the nostril rarely reaches past the anterior margin of the orbit.

**Ichthyscopus spinosus** Mees, 1960
(Figs 2A, 8A)

*Ichthyscopus spinosus* Mees, 1960: 48, figs 1,2. Type locality – near Broome, northwestern Australia.

MATERIAL. Western Australia:- NTMS10959-020 (1, 134) N of Port Hedland, 80m, 18 April 1983, R. Williams, F/V Tung Mao; WAMP14325-001 (1, 165) 16 miles N of Port Hedland, 13 September 1965, H. Kalnins.

DIAGNOSIS. Dorsal fin with II spines and 17.5 soft rays, anterior end differentiated into short anterior segment by deep concavity in distal margin; 3rd element (= 1st soft ray) shortest, anterior segment dark with pale basal margin at least anteriorly; posterior nostril elongate, rimming fleshy anterior gap in bony orbit; labial fimbriae simple, smooth-edged; skin flap adjacent to ventrolateral edge of lower lip with smooth margin; each side of lower jaw with 4 to 6 teeth; chin lacking barbels; cleithral skin flap slightly less than twice length of cleithral spine; fleshy horizontal subcleithral ridge continuing on posterior side of pectoral fin axis from base nearly to tip of cleithral skin flap; crest of ridge irregular but not fimbriate; scales present, in 38-41 oblique rows; numerous small dark spots on upper portion of sides, head and on dorsal, caudal, anal and pectoral fins.

DESCRIPTION. Dorsal fin rays II, 17.5 (anterior elements slender, 3rd an unsegmented, unbranched 'soft ray' which is difficult to distinguish from preceding spines even with use of radiographs; 4th segmented but unbranched; last element shorter than penultimate element and associated with a reduced pterygiophore); anal fin rays 16; caudal fin with 12 principal rays and 3 unsegmented procurrent rays dorsally and ventrally; pectoral fin rays 16 or 17; pelvic fin rays I, 5; vertebrae 9 + 16; epipleural ribs 8, situated on vertebra 5-12.

Body moderately deep, compressed posteriorly; head rather square in cross section (see Table 1 for morphometric data).

Head mostly encased in bone, without obvious joint lines dorsally; bony surface textured with fine low vermiculations; dorsal surface mostly flat, only slightly concave posterior to interorbital fossa. Interorbital fossa rectangular, width posteriorly about 2/3 that between orbits. Orbit circular, diameter distinctly greater than that of eye. Anterior nostril small, approximately 1/4 eye diameter, tubular, divided into 2 openings by midposterior flap; anterior side with low rim providing notch, rim edged with moderately short simple to bilobed fimbriae. Opening of posterior nostril elongate, rimming fleshy anterior gap in bony orbit; nostril with prominent anterior flap and less prominent medial and lateral flaps, each with fimbriate edges; anterior flap functionally dividing nostril into lateral and mesial openings. Both lips with simple, smooth edged fimbriae externally, fimbriae on lower lip occasionally branched at corner of mouth; 25 or 26 individual fimbriae on upper lip, 52 to 55 on lower; skin flap on lower jaw adjacent to ventrolateral edge of lower lip with smooth margin; inner edge of upper lip with sawtooth margin, lower lip without inner fimbriate fringe. Upper jaw with broad band of numerous small slightly curved teeth; teeth not in distinct rows, about 3 or 4 teeth across band where broadest. Lower jaw in

large specimens with 4 to 6 prominent widely spaced straight narrow canines angled back into mouth on each side, posteriormost noticeably longer than others (smaller specimens with up to 8 or 9 teeth on each side of lower jaw). Oral valve broad, fleshy, drawn upwards into a low point medially (1 specimen with simple fimbriate margin). Chin smooth, without barbels. Dorsal half of opercular margin fimbriate, with 21 to 23 individual fimbriae; ventralmost fimbriae simple, those dorsally with up to 4 or 5 very short lateral branches, branches rarely subdivided; opercular margin smooth ventrally.

Cleithral spine extending posteriorly almost to above dorsal extent of pectoral fin axis. Fleshy cleithral skin flap enveloping cleithral spine extending well past this point; underside of flap fimbriate with 15-18 individual fimbriae, including several simple fimbriae anteriorly beneath opercular margin; fimbriae, including that at tip of flap, with up to 2 or 3 very short side branches on both anterior and posterior margins, those closest to tip with most branches, branches rarely subdivided into sub-branches. Narrow fleshy subcleithral ridge extending horizontally from upper angle of opercular opening to dorsal extent of pectoral fin base, continuing on posterior side of pectoral fin axis to just below free posterior tip of cleithral skin flap, forming short free pointed flap posteriorly; crest of ridge with several low bumps, sometimes also having a few simple slender papillae (Fig. 2A). Upper half of opercle and preopercle with low surface vermiculations similar in form but finer in texture than those on dorsal cranial plates; lower halves with simple fine striae radiating ventrally. No spines associated with subopercle, opercle, preopercle or basipterygium.

Dorsal fin rather long-based and low, anterior end partially separated into short anterior segment by concavity in distal margin; 1st 3 dorsal fin elements relatively short, 1st longest, 3rd shortest, 3rd about 4/5 length of 1st and 2nd and slightly more than 1/2 length of 4th; subsequent elements progressively longer. Anal fin long-based and low. Caudal fin truncate to slightly rounded with branched tips of caudal rays extending slightly beyond membrane. Pectoral fin pointed at tip of 5th ray, membrane incised slightly between tips. Pelvic fins strong and fleshy, inner 2 rays longest, interradial membranes more clearly incised in remaining rays. Ventral midline with medial ventral skin flap from anterior tip of basipterygium to rear of pelvic fin base. A small rounded transverse flap posteriorly at midbase of pelvics.

Scales prominent, cycloid, rectangular, arranged in about 38-41 obliquely angled rows, (including smaller scales in less well defined rows on upper corner of caudal peduncle), occasionally, 2 scale rows merging into 1 as they proceed ventrally. Underside of body naked anteroventral to an imaginary line connecting tip of cleithral skin flap and center of anal fin base. Lateral line pores in angled lines or clumps of 3-8 at dorsal end of each diagonal scale row. Nape between rows of lateral line pores devoid of scales; sensory pores absent from nape except for those associated with lateral line, between lateral lines at base of dorsal fin, those on naked skin adjacent to posterior margin of head shield and those piercing head shield posterolaterally.

Colour in alcohol pale brown dorsally on sides and head, white below, numerous deep brown spots with diameters ranging from pupil to eye size on dorsal half of head and body and on dorsal, caudal, anal and pectoral fins; spots on interorbital fossa, lips and chin smaller, some more or less joined to form wavy lines. Dorsal fin pale with dark anterior segment and several series of deep brown spots, comprising a row of rather large spots basally and smaller spots marginally; anterior segment with pale margin anteroventrally. Anal fin pale with midlateral row of small brown spots posteriorly. Caudal fin pale with several large brown spots proximally. Pectoral fin pale with scattered brown spots and tan blotch dorsally near base. Pelvic fins white. Juveniles unavailable. Colour in life unknown.

DISTRIBUTION. Recorded only from the coastal waters of central Western Australia in the region of Port Hedland (22°18'S 118°35'E) and Broome (17°58'S 122°14'E) (Fig. 8A); depth distribution of this species unclear as capture depth for museum specimens only available for 2 specimens (NTMS10959-020 and WAMP14325-001), 1 taken at 80m and the other, according to registration information, buried in an exposed sand bar when collected.

REMARKS. This species is known from only 4 museum specimens. Its rarity in collections is probably more reflective of limited sampling in both the geographical region and habitat where it occurs than the size of the population.

TABLE 2. Distribution of character states for selected variable morphological features in the 6 Australian species of *Ichthyscopus* and the genus *Uranoscopus*.

| Character | *I. barbatus* | *I. fasciatus* | *I. insperatus* | *I. nigripinnis* | *I. sannio* | *I. spinosus* | *Uranoscopus* |
|---|---|---|---|---|---|---|---|
| Lower jaw teeth (many/few) | 2 | 0 | 1 | 2 | 1 | 2 | 0 |
| Labial fimbriae (absent/present) | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Labial fimbriae (simple/branched) | 0 | 1 | 1 | 0 | 1 | 0 | variable |
| Upper labial fimbriae (few/numerous) | 0 | 1 | 1 | 0 | 1 | 1 | variable |
| Opercular margin (exposed/concealed) | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Opercular margin (few/many fimbriae) | 1 | 0 | 1 | 1 | 1 | 1 | variable |
| Cleithral flap (not/well developed) | 2 | 1 | 2 | 2 | 2 | 2 | 0 |
| Sub-cleithral ridge (not/well developed) | 1 | 0 | 1 | 2 | 1 | 2 | 0 |
| Sub-cleithral ridge (no/many fimbriae) | 2 | 0 | 1 | 2 | 1 | 1 | 0 |
| First dorsal on anterior vertebrae (present/absent) | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| First dorsal (present/absent) | 1 | 0 | 0 | 2 | 1 | 2 | variable |
| Dorsal spines (0, 1, 2, 3) | 2 | 1 | 1 | 3 | 2 | 2 | variable |
| Number of pleural ribs (not reduced/ reduced) | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Lateral line on caudal peduncle (unfused/fused) | 1 | 1 | 1 | 1 | 1 | 1 | 0 |

## OTHER MATERIAL EXAMINED

*Ichthyscopus* sp. JAPAN:- CAS-SU7015 (1, 257) Wakanoura, D. Jordan & J. Snyder; TAIWAN: CAS28205 (1, 48.1) South China Sea, SW of Kao-Hsiung, 70-90m, 13 October 1972, F. Steiner; MALAYSIA: CAS35867 (1, 163) Borneo, off Kuching, 40-50m, November, 1975, F. Steiner.

*Ichthyscopus lebeck*, INDIA: AMSB7519 (1, 220) Malabar, F. Day; CAS-SU41734 (1, 173) Madras Pres., Ennur Fisheries Station, January 1941, A.W. Herre.

## RELATIONSHIPS AND BIOGEOGRAPHY

A comparison of 14 variable characters present in the Australian species of *Ichthyscopus* and *Uranoscopus* (Table 2) using PAUP yielded 2 trees having an equal shortest length of 22 steps with a consistency index of 0.909. A strict consensus of these 2 trees is presented as Fig. 9A, with the preferred tree as discussed below shown as Fig. 9B. As pointed out in the above discussion of *I. fasciatus*, the primitive structure of the fleshy flap on the cleithral spine, absence of any subcleithral ridge development in association with it, and the large number and uniform size of lower jaw teeth relative to those in other species of *Ichthyscopus* support an initial divergence of *I. fasciatus* from the line giving rise to the remaining 5 species, all sharing derivations of these features. A subsequent divergence of *I. insperatus* is supported by the absence of any sign of the differentiation of a dark anterior segment of the dorsal fin, as found in the remaining 4 species, a character which is likely to be a modification for that line. The succeeding divergence of *I. sannio* is supported by the larger number of lower jaw teeth relative to the remaining 3 species. This species also shares branched fimbriae on the lips with *I. fasciatus* and *I. insperatus* rather than having the simple fimbriae of the last 3. Even though the fringed character state may appear to be apomorphic because of its complexity, it is more likely to be primitive for the genus and determined by the nature of the substrate in which the species regularly bury themselves. Although the distribution of characters in *I. barbatus*, *I. nigripinnis* and *I. spinosus* do not provide a clear indication of relationships in the analysis, the greater development of the unique subcleithral ridge and better developed anterior segment of the dorsal fin in *I. nigripinnis* and *I. spinosus* support a paired relationship of the 2 (Fig. 9B). Despite the remarkable similarity of pigmentation in *I. barbatus* and *I. nigripinnis*, the general elements of the pattern (i.e. dark saddles on the body) are also present to some degree in both *I. spinosus* and *I. sannio*, suggesting they are features that occurred in the ancestor of all four.

Although the two northern hemisphere species of *Ichthyscopus* were not included in this analysis, a superficial examination of specimens of both indicates they are likely to constitute a monophyletic line which diverged after the separation of *I. insperatus*, but prior to the divergence of *I. sannio*. This is supported by the absence of any development of a separate

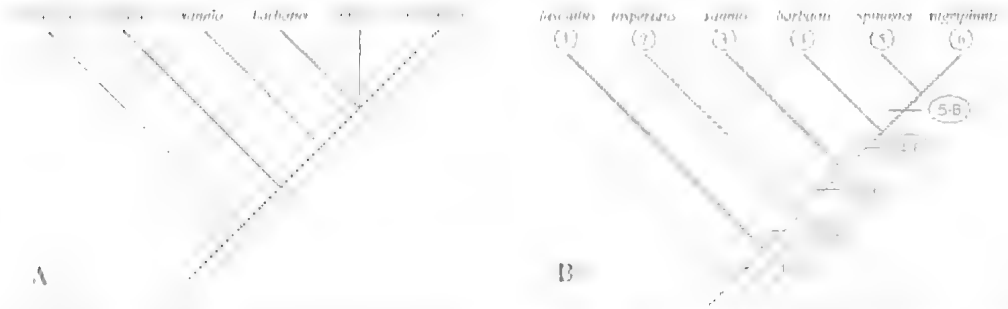



FIG. 9. Hypothesised relationships of Australian species of *Ichthyscopus* relative to the arbitrary outgroup *Uranoscopus* A, strict consensus, and B, preferred.

anterior segment of the dorsal fin in the first two, which is present in *I. sannio* and subsequently diverging species. Still, the presence of a darkened area at the anterior end of the dorsal fin in a 43mm SL specimen of the NW Pacific species may represent the first stages of this development. The two northern hemisphere species share a unique crenulated margin on the opercular membrane anterior to the pelvic fin bases, which is best developed in *I. lebeck*. This feature is absent in Australian species.

Unlike the speciose genus *Uranoscopus* with its numerous true tropical representatives, most if not all species of *Ichthyscopus* are, at the very least, antitropical in distribution. None of the species occur in both the southern and northern hemispheres. The genus *Astroscopus* hypothesised by Pietsch (1989) as sharing an immediate common ancestry with *Ichthyscopus* is similar in this regard, although one of the two recognised Atlantic species and the sole Pacific representative is reported to occur on both sides of the equator. Judging from the current distribution of the species in these two genera with the majority of the species of *Ichthyscopus* confined to Australasia, it is likely that the ancestor common to the two taxa had a southern hemisphere distribution. It is also likely that the New Zealand genus *Genyagnus*, thought to share an immediate common ancestry with the *Astroscopus*/*Ichthyscopus* line (Pietsch, 1989), diverged at about the same time. The establishment of the Southern Sub-Tropical Convergence as a result of the expansion of the Antarctic ice cap in the late Miocene (~ 5 million years before present) had major biogeographical affects (Frakes et al., 1992) and may have been involved. It is noteworthy that apart from *Uranoscopus* and the two genera, *Astroscopus* and the recently described, monotypic *Selenoscopus* (Okamura & Kishimoto, 1993), which are equally diverse in the two hemispheres, the greatest diversity of stargazer genera is in the southern hemisphere (and more specifically the Australasian region), with two of the five, the monotypic *Genyagnus* and *Pleuroscopus*, totally confined to southern latitudes.

The relatively localised distributions of *Ichthyscopus* species may provide an insight into at least one mechanism for speciation in the Australian region. Of the six Australian species, two are confined to the west coast of Australia and two to its east coast, with a fifth traversing the northern coast and the sixth distributed in the south (Fig. 8). The southern species spanning the width of the Australian continent has a disjunct distribution which may lead to differentiation in the future. The absence of any species of the genus in equatorial or cold temperate waters suggests that temperature is at least in part a factor affecting the extent of distribution. This affect is also apparent in the ranges of east and west coast species. It is likely that periods of latitudinal shift in isotherms associated with periodic cooling and warming of southern waters have driven populations possessing discrete temperature tolerances northwards and southwards along the Pacific and Indian Ocean coasts of Australia. Cycles of climatic fluctuations have occurred at approximately 100,000 year intervals through the late Quaternary with the last major interglacial period having taken place about 122,000 years ago (Frakes et al., 1992). Although historical patterns of water mass circulation in the Indian and Pacific Ocean basins are far from clear, it is likely that, as today, population expansions into southernmost or northernmost waters have been able to proceed more easily in an easterly or westerly direction depending on conditions of water movement existing at the time. Thus populations on either side of the continent when forced into southern or northern latitudes may not have had the same likelihood of reaching the opposite coast.

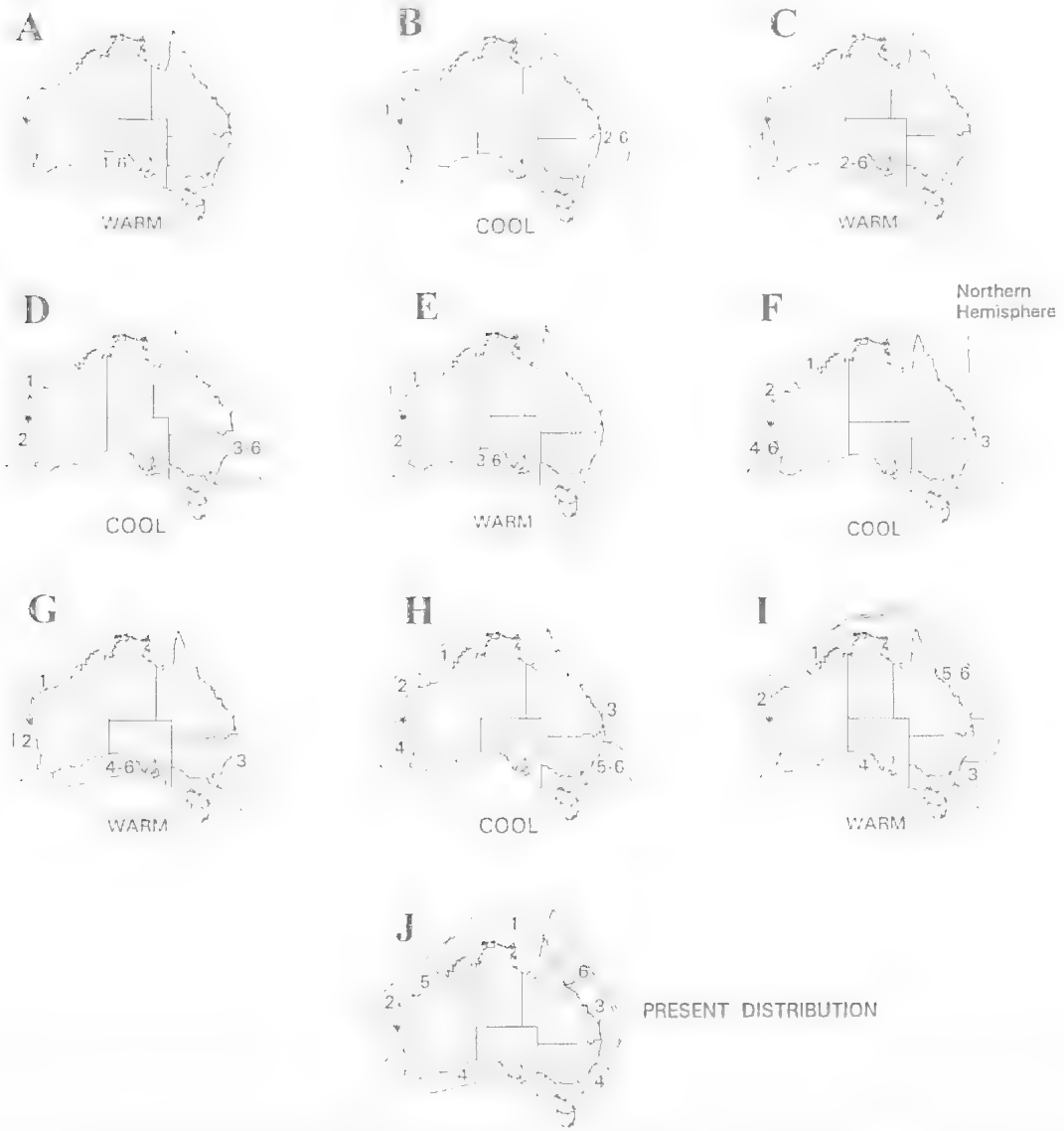



FIG. 10. Hypothesised sequence of ancestral distributions A-I, effected by periodic warming and cooling events in the Southern Hemisphere, leading to current species distributions, J. Numbers on distributional ranges of populations correspond with those of Fig. 9B.

With respect to the species relationships represented in Fig. 9B, the presence of the initial two diverging species, *I. fasciatus* and *I. insperatus*, in tropical, northwestern Australian waters, but the absence of *I. insperatus* or a sister taxon from northeastern waters supports an hypothesis that the southern coast was the side of the continent involved in the east-west expansion of populations. Likewise, the absence of any further speciation of the *I. fasciatus*-line (assuming that extinction did not occur) points to an historic presence in the northwest and only a recent expansion of the range of this species into the Pacific. An hypothesis of sequential changes in population distributions and the subdivision of populations caused by periodic warming and cooling shifts in southern hemisphere climates would explain the current distribution of taxa as presented in Fig. 10. Numbers superimposed on populations represented in this figure correspond with those in Fig. 9B. Although this is not the only hypothesis which would account for current distributions, it

requires no extinctions and assumes that all but the present longitudinal range expansion occurred across a single (the southern) coast.

If *I. sannio* is indeed the species closest to the Japanese and NE Indian Ocean taxa as has been implied by previous treatments of this genus, the transgression of an equatorial barrier by this taxonomic line is likely to have occurred prior to the differentiation of *I. nigripinnis* and *I. spinosus*, and perhaps that of *I. barbatus* (Fig. 10F). In addition, it is likely that this transgression took place in the W Pacific, accompanied by a subsequent expansion of the NW Pacific population into the Indian Ocean. The last hypothesis is supported by the presence of numerous other anti-tropical east Australian/ Japanese cognate species pairs which lack close relatives in the NE Indian Ocean. Many of these cognates have only recently been recognised as specifically different.

The greater latitudinal range of *I. nigripinnis* relative to shallower dwelling species in the genus, especially *I. sannio*, with which it is geographically sympatric, may be associated with its rather deep bathymetric distribution and the greater continuity of suitable habitats with relatively little temperature fluctuations which are present at greater depths. This penchant for deep cool waters is shared by *I. barbatus*. The virtual absence of information on the ecological propensities of *I. spinosus* makes it difficult to assess the hypothesis that this form of distribution is an ancestral trait.

## ACKNOWLEDGEMENTS

Specimen loans were facilitated by M. McGrouther (AMS), H. Larson (NTM), T. Sim and the late C.J.M. Glover (SAM), T.W. Pietsch (UWS) and S. Morrison (WAM). Access to CAS material was provided by W. Eschmeyer and T. Iwamoto. We are particularly grateful to K. Graham (NSW Fisheries) who recognised the status of *I. nigripinnis* and made a concerted effort to lodge representative material in the Australian Museum. Radiographs were prepared by T. Bardsley (NMV) and J. Fong (CAS). Assistance with the phylogenetic analysis came from A. Reid. Comment on non-Australian species of the genus was kindly provided by H. Kishimoto, while G. Nelson and D. Bray made useful suggestions for improvements to the manuscript.

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**DESIGNATION OF A LECTOTYPE FOR THE PLATYCEPHALID FISH *INEGOCIA HARRISII* (McCULLOCH).** *Memoirs of the Queensland Museum 43(2): 620. 1999*:- McCulloch (1914) described *Insidiator* (=*Inegocia*) *harrisii* from 2 specimens, one from off Pine Peak, Qld and the other from Moreton Bay, Qld. He also made mention of 5 additional (non-type) specimens that were trawled off Bowen, Qld. According to Paxton et al. (1989: 466) and McGrouther et al. (1998) the 2 syntypes are in the Australian Museum, registered AMSE2844 (Pine Peak specimen) and AMSI12765 (Moreton Bay specimen). Eschmeyer (1998), however, lists AMSI12765 and AMSI12805 as syntypes and AMSE2844 and QMI1437 as non-type material.

Collection data indicates that AMS12805 and QMI1437 were taken aboard the F.I.S. Endeavour off Bowen. At about 196 and 191mm TL they are of intermediate length to that given for the syntypes (183 and 204mm). It appears therefore that Eschmeyer is partially in error and that these specimens are probably the non-type material mentioned by McCulloch.

The distribution of *Inegocia harrisii* was recognised by Paxton et al. (1989: 466) as from N Australian waters between Napier Broome Bay, WA (126°36'E) and off Pine Peak, Qld (21°23'S). *Inegocia japonica* (Tilesius) is commonly taken by trawl in Moreton Bay, but often appears to have been misidentified from this area as *I. harrisii* (see Stephenson & Burgess, 1980; Stephenson et al., 1982; Johnson, 1999). The syntype of *I. harrisii* from Moreton Bay, at approximately 27°15'S, is well south of other confirmed records of the species. Both syntypes were examined to determine the reasons for this anomaly. From the characters below, AMSI12765 was identified as a specimen of *I. japonica*. It has 19 pectoral rays, 12 second dorsal and anal fin rays and a distinct interopercular flap. AMSE2844 has 25 pectoral rays, 11 dorsal and anal rays and lacks an interopercular flap. This determination was confirmed from unpublished notes by Dr Les Knapp (pers. comm., 1996). Knapp (unpubl.) advised that *I. harrisii* may be separated from *I. japonica* on pectoral ray counts (22-25 vs 18-21), dorsal and anal rays (usually 11 vs usually 12), interopercular flap (absent vs present) and the number and position of spines on the suborbital ridge .

To fix the specific name AMSE2844 is here designated lectotype of *I. harrisii* (McCulloch).

**Acknowledgements**

Thanks are due to Mark McGrouther (Australian Museum) for providing collection data on, and the loan of, type specimens. Dr Leslie Knapp (National Museum of Natural History, Washington) kindly assisted with unpublished notes on the syntypes and diagnostic information on platycephalids.

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# FIVE SPECIES OF KLEPTOBIOTIC *ARGYRODES* SIMON (THERIDIIDAE: ARANEAE) FROM EASTERN AUSTRALIA: DESCRIPTIONS AND ECOLOGY WITH SPECIAL REFERENCE TO SOUTHEAST QUEENSLAND

PAUL GROSTAL

Grostal, P. 1999 06 30: Five species of kleptobiotic *Argyrodes* Simon (Theridiidae: Araneae) from eastern Australia: descriptions and ecology with special reference to southeast Queensland. *Memoirs of the Queensland Museum* **43**(2): 621-638. Brisbane. ISSN 0079-8835.

Many spiders of the genus *Argyrodes* Simon (Theridiidae) live on webs of large spiders and steal food (kleptobiosis). Although more than 45 species of *Argyrodes* may occur in Australia, little is known of their taxonomy and ecology. I provide diagnoses, geographical distributions and notes on ecology of 5 *Argyrodes* species commonly found on webs of orb weavers in southeast Queensland. Of these, previously named species include *A. antipodianus* Pickard-Cambridge, *A. miniaceus* (Doleschall), *A. rainbowi* (Roewer) and *A. fissifrons* Pickard-Cambridge. *A. musgravei* Rainbow is synonymised with *A. miniaceus*. A new species, *A. alannae* is described. ❐ *Argyrodes, kleptoparasite, kleptobiosis, host, Theridiidae, spider, ecology, systematics, Australia.*

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*Argyrodes* species (Theridiidae) are small spiders, found mostly in the tropics and subtropics throughout the world (Exline & Levi, 1962; Levy 1985). Two genera, *Rhomphaea* L. Koch and *Ariamnes* Thorell, are presently included in *Argyrodes* (Levi & Levi, 1962). The synonymised genera were distinguished by the clypeal modification of male cephalothorax, eye arrangement and relative length of metatarsi (Simon, 1894), but Levi & Levi (1962) noted that these characters did not reliably separate the taxa.

Many species of *Argyrodes* are known to be closely associated with large orb-weavers and other web-building spiders (Exline & Levi, 1962; Vollrath, 1984; Vollrath, 1987; Elgar, 1993). These small web inhabitants rarely catch their own food, but instead specialise in the removal and consumption of prey caught in webs of their hosts. This unusual foraging behaviour has earned them the name of 'kleptobionts' or 'kleptoparasites' (Vollrath, 1984, 1987; Elgar, 1993). However, the ecology of kleptobiotic *Argyrodes* and the nature of their relationship with hosts are little known (Elgar, 1993).

Little information is available on the taxonomy of Australian species of *Argyrodes*. Over 45 species may occur in Australia (Roewer, 1942; Bonnet, 1957; Brignoli, 1983; Platnick, 1987; Platnick, 1991), but only one taxonomic paper that included Australian collections (Gray & Anderson, 1989) has been published since 1916. I diagnose 5 species of *Argyrodes* that are commonly associated with orb-weaving spiders in southeast Queensland, with the distribution of these kleptobionts in eastern Australia and with notes on their ecology, including host-specificity.

## METHODS

*Terminology*. In the female: insemination duct joins gonopores to spermathecae; fertilisation duct joins spermathecae to ovaries. In the male: cephalic projection is the upper frontal cephalothoracic projection, bearing median eyes; clypeal projection is the lower frontal cephalothoracic projection (arising underneath cephalic projection), without eyes.

Names of sclerites of male palpal bulb (Fig. 2F) follow Coddington (1990), who disputed some earlier terminology. For example, he suggested that the sclerite termed 'median apophysis' by Exline & Levi (1962) was an autapomorphic outgrowth of the tegular wall, and renamed it 'tegular apophysis'. The sclerite contains a loop of the seminal duct (Fig. 2F). Further, Coddington proposed that Exline & Levi's 'radix' might be '... the median apophysis (in a developmental sense).' Here, I call it the extension of median apophysis. All specimen measurements are given in mm.

*Abbreviations*. Institutions: AM, Australian Museum, Sydney; HEC, Hope Entomological Collection, Oxford University Museum, Oxford,

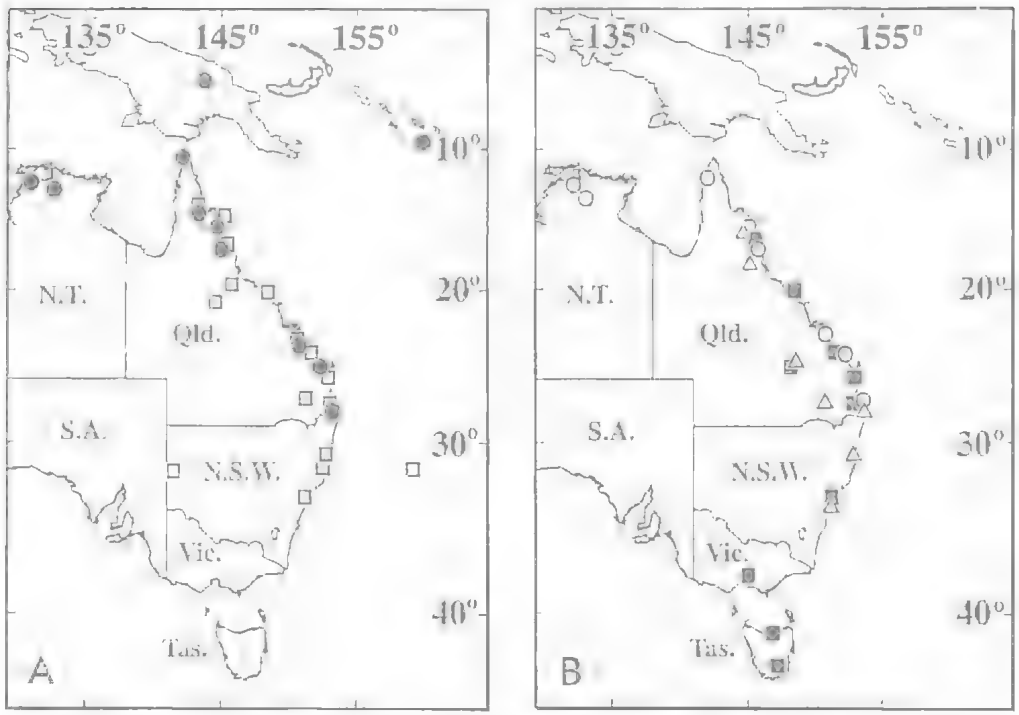



FIG. 1. Collection localities of five species of *Argyrodes* from AM and QM collections. *A. antipodianus*; *A. miniaceus*; ∇ *A. rainbowi*; ■ *A. alannae*; ○ *A. fissifrons*.

UK; NHMW, Naturhistorisches Museum, Wien, Austria; QM, Queensland Museum. Morphology: AME, Anterior median eyes; PME, Posterior median eyes; ALE, Anterior lateral eyes; PLE, Posterior lateral eyes; AL, abdomen length; AH, abdomen height; AI, abdomen index; CL, carapace length; CI, carapace index.

## SYSTEMATICS

### **Argyrodes** Simon, 1864

*Argyrodes* Simon, 1864: 253. Type species by tautonymy *Linyphia argyrodes* Walckenaer, 1841 (Levy, 1985). Synonymy follows Levi & Levi (1962).

DESCRIPTION. (from Exline & Levi, 1962; Levy, 1985). Cephalothorax: male carapace with a projecting cephalic and/or clypeal region, otherwise with a deep seam under anterior median eyes. Female carapace relatively flat, without projections or fissures. Chelicerae with several teeth. Legs: 1st pair longest, 2nd and/or 4th second in length, 3rd shortest. Comb setae on 4th tarsus usually absent, but serrated bristles usually present. Third tarsal claw longer than paired. Male palp: cymbium with small hook (paracymbium, Fig. 2F) behind bulb, on edge of alveolus. Abdomen shape variable, but rarely oval; sometimes conical/triangular (higher than long), or vermiform (e.g. *Ariamnes* species group), often extending beyond spinnerets. Fleshy colulus (usually with two short setae) in front of spinnerets. Silver-coloured speckles of varying density on abdomen of many species.

REMARKS. The five species described herein are not the only kleptobiotic species of *Argyrodes* in southeast Queensland. Two other species: *A. kulczynskii* (Roewer, 1942) and an undescribed species (sp. 1) occur on webs of other spiders and were also collected in the area (QM). Consequently, this paper is not a geographic review, but a description of five common species. I distinguish the described species from other sympatric or related species in the Diagnoses. The taxonomy of the remaining two species is currently being studied.

*Characters common to the five species.* Abdomen never vermiform (e.g. *A. colubrinus* (Keyserling, 1889); see Ecology and Behaviour) and without hooks on apex. For males, extension of median apophysis is denticulate distally. Unlike males of species 1 (undescribed, QM

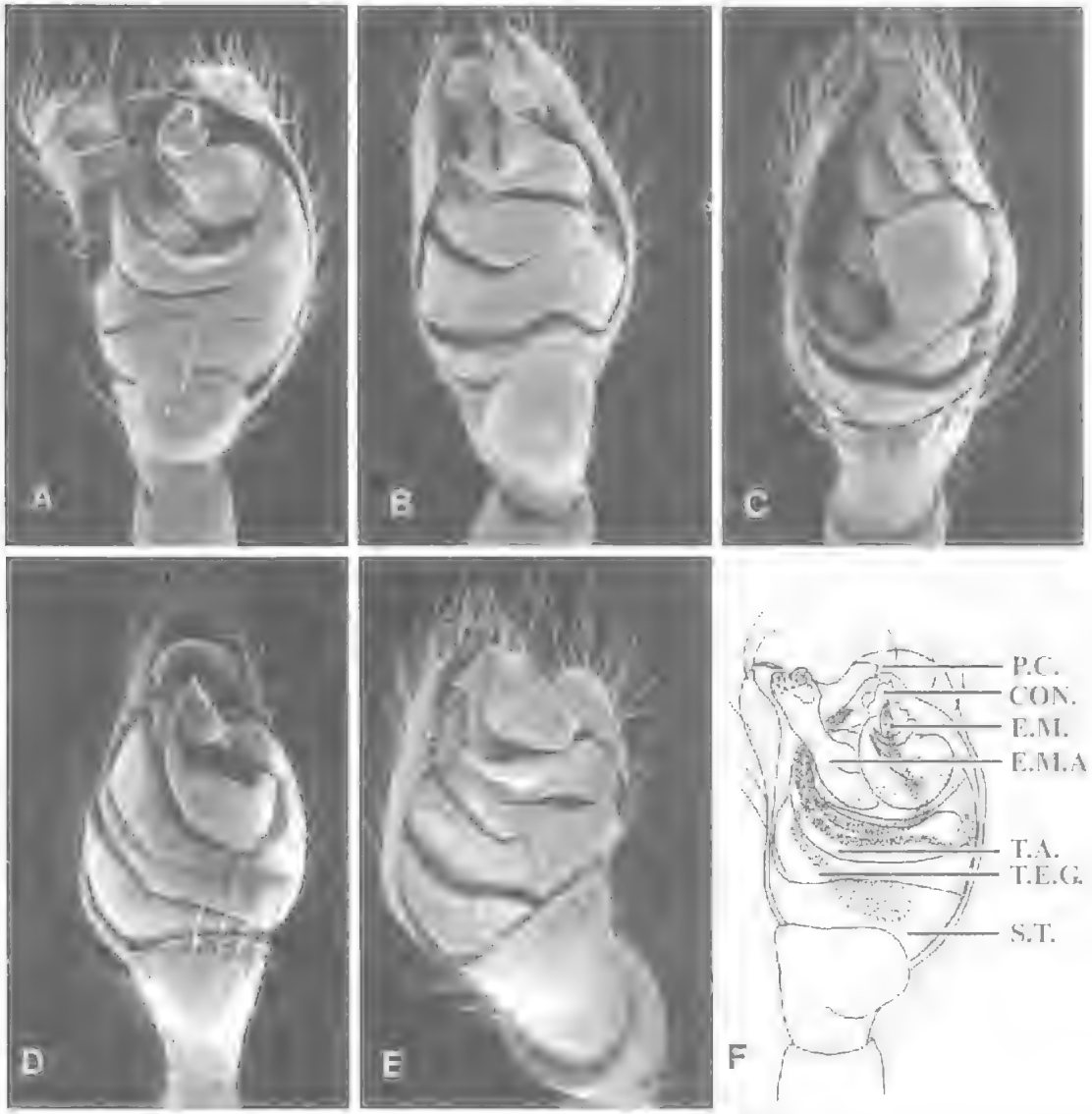



FIG. 2. Scanning electron micrographs of male palps. A, *A. antipodianus*; B, *A. miniaceus*; C, *A. rainbowi*; D, *A. alannae sp. nov.*; E, *A. fissifrons*.F, *A. antipodianus*, P.C. = paracymbium, CON. = conductor, EM. = embolus, E.M.A. = extension of median apophysis, T.A. = tegular apophysis, TEG. = tegulum, S.T. = sub-tegulum, stipled section = seminal duct.

S42030) which lack a clypeal projection, males of all five species described below have both clypeal and cephalic projections (for *A. rainbowi* and *A. kulczynskii* the projections appear fused).

### Argyrodes antipodianus
Pickard-Cambridge, 1880
(Figs 2A,F, 3A-K)

*A. antipodiana* Pickard-Cambridge, 1880: 327; Bonnet, 1957 (=*A. antipodianus*): 707.

*A. conus* Urquhart, 1884: 40, pl. 10, fig. 6 (first synonymised by Dalmas, 1917).

*Argyrodina antipodiana* Roewer, 1942: 434.

MATERIAL. TYPES: *A. antipodianus* (*-na*) Pickard-Cambridge, 1880, (presumed types; see Remarks), F's. juv., New South Wales, Australia (bottle 555, tube 19), New Zealand (bottle 555, tube 13) (HEC). OTHER MATERIAL: New South Wales - AMKS9387, M. Taree, 31°53'S, 152°29'E; AMKS49165, Currawong, Broken Bay, 33°36'S, 151°18'E; AMKS49166, Scone, 32°03'S, 150°52'E; AMKS49167, Petersham, 33°53'S, 151°09'E;

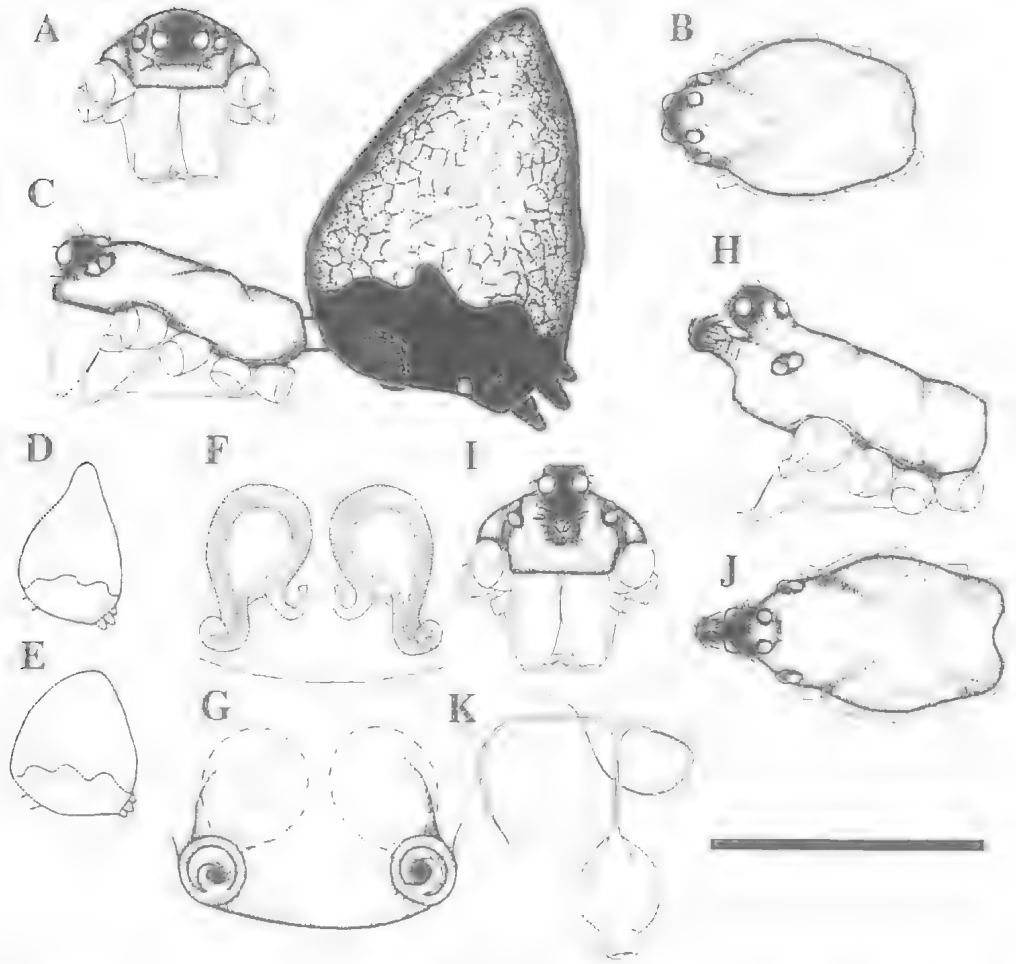



FIG. 3. *A. antipodianus*. A-C, female cephalothorax and abdomen; D, E, variation in shape of female abdomen; F, spermathecae and fertilisation ducts; G, epigyne; H-J, male cephalothorax; K, egg sac. Scale bars: A-D, G, H = 1.2mm; D, E = 4.7mm; F, G = 0.229mm; K = 7.9mm.

AMKS49168, F, Pittwater, 33°38'S, 151°18'E; AMKS49171, F, Wagstaff, 33°32'S, 151°21'E; AMKS49172, M, F, Broken Hill, 31°58'S, 141°27'E; QMS29895, M, Turners Dip, 31°01'S, 152°42'E; QMS46645, M, Sydney, 33°53'S, 151°13'E. Queensland - AMKS12818, M, F, Mt Drylander, via Proserpine, 20°15'S, 148°32'E; AMKS17588, F, Fitzroy I., 16°56'S, 146°00'E; AMKS19744, F, Fletchers Ck, via Charters Towers, 19°49'S, 146°03'E; AMKS49147, F, Lizard Island, Great Barrier Reef , 14°40'S, 145°28'E; AMKS49154, M, F, Mossman, 16°28'S, 145°28'E; AMKS49158, F, Edmonton, 17°01'S, 145°45'E; QMS29823, M, Freshwater Ck, Cairns, 16°55'S, 145°41'E; QMS29839,F, Qld; QMS29840, 2F, Bundaberg Forest, 24°52'S, 152°21'E; QMS29846, 2M, 2F, North Keppel I., 23°04'S, 150°53'E; QMS29848, F, QMS29944, F's, Kroombit Tops, 24°22'S, 151°01'E; QMS29850, M, F, Eureka Ck, 17°09'S, 144°59'E; QMS29855, M, Majors Mt, 17°37'S, 145°32'E; QMS29859, F, Double I., Cairns, 16°44'S, 145°41'E; QMS29861, F, Yungaburra, 17°17'S, 145°35'E; QMS29887, M, Peak Downs, 22°15'S, 148°11'E; QMS29896, 5F, Coen, 13°56'S, 143°12'E; QMS29899, 2M, F, Mt Garnet, 17°41'S, 145°07'E; QMS29939, M, 2F, Chillagoe, 17°09'S, 144°31'E; QMS29940, 2F, Lake Broadwater, via Dalby, 27°20'S, 151°05'E; QMS29941, F, D'Aguilar, 26°59'S, 152°48'E; QMS29942, F, Hughenden, 20°51'S, 144°12'E; QMS46598, M, QMS46599, M, QMS46648, F, Pinkenba, Brisbane, 27°26'S, 153°07'E; QMS46605, M, QMS46606, M, QMS46634, F, QMS46635, F, QMS46642, 2M, 3F, Yeppoon, 23°08'S, 150°45'E; QMS46608, M, QMS46609, M, QMS46630, F, Cairns, 16°55'S, 145°46'E; QMS46611, M, QMS46628, F, QMS46629, F, QMS46652, 17F, Gladstone, 23°51'S, 151°16'E; QMS46617, F, QMS46619, F, QMS46622, F,

QMS46643, 4F, QMS46644, 10F, 1 juv., Nathan, Brisbane, 27°33'S, 153°03'E; QMS46625, F, QMS46641, 2F, QMS46646, M, 2F, North Stradbroke I., 27°35'S, 153°27'E; QMS46626, F, QMS46649, 3M, 9F, Kabra, 23°28'S, 150°24'E; QMS46627, F, Chapel Hill, Brisbane, 27°28'S, 153°03'E; QMS46638, M, 2F, St Lucia, Brisbane, 28°27'S, 153°01'E.

DIAGNOSIS. Abdominal colour (bright silver), combined with morphologies of male palp, male carapace and epigyne separate *A. antipodianus* from other sympatric species. Palpal cymbium conspicuously bi-lobed, base of embolus with two pointed projections, extension of median apophysis narrow and concave distally (Fig. 2A,F). Lateral eyes (ALE and PLE) of males below base of cephalic projection (character shared by *A. miniaceus*), but clypeal projection club-shaped and with pectinate setae (Fig. 3H-J) contrasting with remaining species (including *A. miniaceus*). Epigynal fossae conspicuous, circular and (unlike remaining species) separated by about twice their diameter (Fig. 3G). Unlike for *A. rainbowi*, *A. fissifrons* or *A. kulczynskii*, insemination duct is short and slightly curved (Fig. 3F). *Argyrodes argentatus* Pickard-Cambridge, 1880 (see Remarks) closely resembles *A. antipodianus* in size, shape and colour, but differs in shape of male carapace. Cephalic projection of *A. argentatus* (lectotype, East Indies, HEC) curves downward and touches (or almost touches) clypeal projection distally (this character is not clear in the illustration of *A. argentatus* by Exline & Levi (1962; fig. 148)), but cephalic projection of *A. antipodianus* is approximately straight and conspicuously separated from clypeal projection (Fig. 3H).

DESCRIPTION. *Male*. Total length 2.35-2.97 (n=13). CL 1.23-1.66, CI 1.63-1.87, AL 1.12-1.83, AI 1.05-1.39, AH 1.37-2.00, Palp 1.29-1.74, leg I 5.00-7.98, leg II 3.03-5.03, leg III 1.72-2.49, leg IV 2.46-3.60. Leg formula 1243. Cymbium length ca. 0.6, width ca. 0.4.

Colour of carapace dark brown, darker around AME and ALE; legs yellowish, pale brown near joints; palps yellowish, except for tarsus (dark brown/black); sternum black to brown; abdomen bright silver dorsally; black mid-dorsal band about as thick as tibia IV originating at pedicel and usually reaching tip of abdomen. A dark spot on abdominal tip of most specimens, but sometimes not clearly visible (perhaps faded in preservative). Ventral surface black to about 1/3 of height of abdomen (see female, Fig. 3C). Two lateral, bright silver spots between epigyne and spinnerets on ventral abdomen.

Abdomen conical/triangular, dorsal tip usually not extending posteriorly beyond spinnerets.

*Female*. Total length 2.57-3.29 (n=13). CL 1.09-1.26, CI 1.24-1.62, AL 1.46-2.83, AI 1.04-1.28, AH 1.77-4.23. Palp 8.30-1.00, leg I 5.32-6.26, leg II 3.55-4.03, leg III 1.77-2.32, leg IV 2.97-3.37. Leg formula 1243. Epigyne width ca. 0.3.

Colour as for male, except both tibia and metatarsus of palp are dark brown. Carapace relatively wide (see CI). Abdomen cone-shaped (Fig. 3C). Epigyne with thickened lateral ridge.

Egg sac chamber urn-shaped, globular, ca. 3.5 long, 2.5 wide; exit hole relatively wide (Fig. 3K).

DISTRIBUTION AND ABUNDANCE. Eastern Australia, Lord Howe I., New Zealand (Pickard-Cambridge, 1880; Urquhart, 1884; pers. obs.).

In Australia, specimens have been collected from warm temperate coastal regions (e.g. Sydney, NSW) to the tropics (e.g. Coen, north Qld). The spider has also been found in relatively dry, inland areas (e.g. Broken Hill, NSW) (Fig. 1A). This is probably the most common species of kleptobiotic *Argyrodes* in southeast Queensland, where adults can be abundant throughout the year.

REMARKS. Bonnet (1957) pointed out that the name *Argyrodes* is masculine, and changed the original name to *A. antipodianus*. A holotype of *A. antipodianus* was not designated by Pickard-Cambridge (1880) (M. Atkinson, pers. comm.), but collector and locality data (H.H.B. Bradley, NSW and F.W. Hutton, New Zealand) of females from HEC match those in the original description. Conspecificity with Pickard-Cambridge's material was established on the basis of female characteristics, as the original collection did not include males.

I did not examine the material collected by Rainbow (1902: 524), Rainbow (1916: 50), Dalmas (1917: 353, fig. 29) and Berland (1924: 197, fig. 65), and the literature did not provide sufficient data to establish conspecificity with the specimens described here. However, the carapace of males from New Caledonia, identified as *A. antipodianus* by Berland (1924), is very similar to that of males from the Australian collections. Specimens of *A. argentatus* were collected from Papua New Guinea (Chrysanthus, 1975) and perhaps are also found in northern Australia. I could find no difference in epigyne

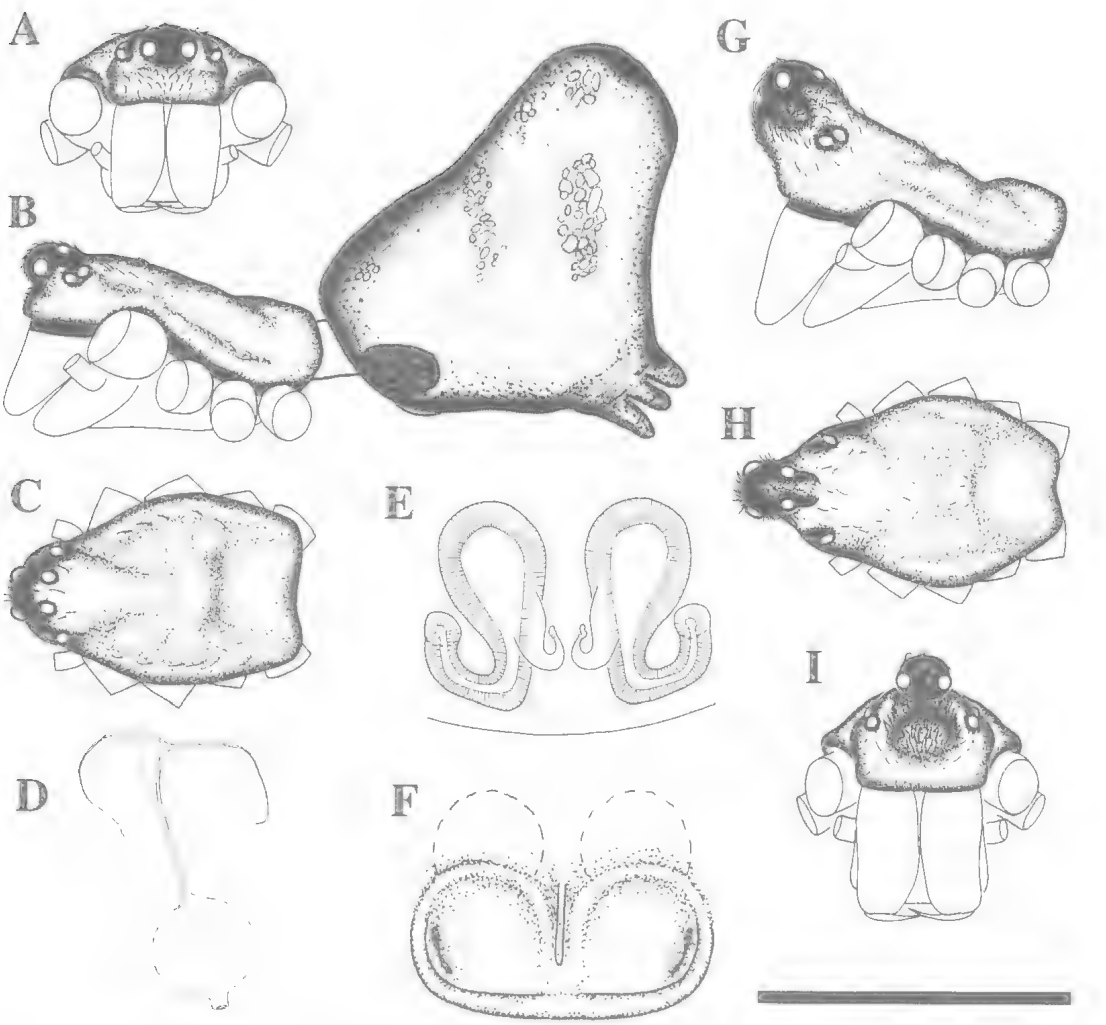



FIG. 4. *A. miniaceus*. A-C, female cephalothorax and abdomen; D, egg sac; E, spermathecae and fertilisation ducts; F) epigyne; G-I, male cephalothorax. Scale bars: A-C, G-I = 2.0mm; D = 13.9mm; E, F = 0.495mm.

morphology between *A. antipodianus* and *A. argentatus*, as the epigynes of *A. argentatus* (Sri Lanka, HEC) were covered with a resinous accretion (also see Levi et al., 1982). None of the Australian male specimens that I examined (including ones from far north Queensland, AM, QM) belong to *A. argentatus*.

### **Argyrodes miniaceus** (Doleschall, 1857) (Figs 2B, 4A-I)

*Theridion miniaceum* Doleschall, 1857: 408 (first synonymised by Thorell, 1878).
*Argyrodes miniaceus*: Thorell, 1878: 138; Berland, 1938: 162; Bonnet, 1957: 715; Chrysanthus, 1963: 739, fig. 63-66, 69; Chikuni, 1989: 177, fig. 22; Platnick, 1987: 192; Platnick, 1991: 191.
*Argyrodina miniacea* Roewer, 1942: 433.
*Argyrodes walkeri* Rainbow, 1902: 524, plate 28, figs 2,3 (first synonymised by Berland, 1938).
*A. musgravei* Rainbow, 1916: 52, plate 15, fig. 28 (new synonymy).

MATERIAL. HOLOTYPE: *A. musgravei* Rainbow, 1916, F, Gordonvale, Qld, Australia (AM). *Theridion miniaceum* Doleschall, 1858, (TYPE), juv. F, Amboina (NHMW). *A. walkeri* Rainbow, 1902, (TYPE), F, Torres I., Torres Strait, Australia (AM). OTHER MATERIAL: AMKS8257, M, F, juv., Cattle Co. Headquarters, Jimi R. (PNG), 05°18'S, 144°14'E; AMKS35057, F, Honiara (Solomon Is), 09°28'S, 159°57'E. Queensland - AMKS49156, M, Mossman, 16°28'S, 145°28'E; AMKS49161, F, Cooktown, 15°28'S, 145°15'E; QMS29822, M, QMS29824, F, Freshwater Ck, Cairns, 16°56'S, 145°42'E; QMS29831, M, QMS29834, F, QMS29836, F, Centenary Lks, Cairns, 16°55'S,

145°46'E; QMS29865, M, F, Carlisle I., 20°47'S, 149°17'E; QMS29866, M, Canal Ck road crossing, Cape York, 11°25'S, 142°23'E; QMS29872, M, F, Bundaberg Forest, 24°52'S, 152°21'E. QMS29879, F, Jardine R., Cape York, 11°09'S, 142°22'E; QMS29883, F, Normanby Stn, 80km NW Cooktown, 15°23'S, 144°52'E; QMS29884, F, Horn I., Torres Strait, 10°37'S, 142°17'E; QMS29886, M, F, Tanners Ppty, Cooktown, 15°30'S, 145°22'E; QMS29890, F, Prince of Wales I., Torres Strait, 10°41'S, 142°09'E; QMS29891, M, F, Jardine R., Cape York, 11°09'S, 142°22'E; QMS29892, 2M, 2F, Port Stewart, 14°04'S, 143°41'E; QMS46514, F, QMS46518, F, QMS46565, M, QMS46566, M, North Stradbroke I., 27°35'S, 153°27'E; QMS46519, F, Pinkenba, 27°25'S, 153°07'E; QMS46520, F, QMS46578, M, The Gap, Brisbane, 28°27'S, 153°01'E; QMS46521, F, Cairns, 16°55'S, 145°46'E; QMS46523, F, QMS46525, F, QMS46570, M, QMS46572, M, Yeppoon, 23°08'S, 150°45'E; QMS46526, F, QMS46574, M, QMS46576, M, Cairns, 16°55'S, 145°46'E. Northern Territory - QMS29873, F, West Alligator R. mouth, 12°12'S, 132°13'E; QMS29874, M, juv., Kemp Airstrip, 12°35'S, 131°20'E; QMS29875, 2M, 2F gorge NE of Mt Gilruth, 13°02'S, 133°05'E; QMS29876, 2M, 2F, QMS29885, F, Radon Ck., 12°45'S, 132°53'E; QMS29877, F, juv., East Alligator R. crossing, 12°25'S, 132°58'E.

DIAGNOSIS. Combination of male carapace, male palp and epigyne morphologies is diagnostic among SE Queensland species. ALE and PLE of males below base of cephalic projection (Fig. 4G,I) (similar to *A. antipodianus*), but unlike all species, clypeal and cephalic projections touch distally (but not centrally, e.g. *A. rainbowi*) (Fig. 4G). Extension of median apophysis relatively broad and convex distally, embolus short and claw-like (Fig. 2B). Fossae large and closely-spaced, almost touching (similar to *A. fissifrons*), but spherical (not reniform, e.g. *A. fissifrons*), with slit-like gonopores (Fig. 4F). Insemination duct short (Fig. 4E), unlike *A. rainbowi*, *A. kulczynskii* or *A. fissifrons*.

DESCRIPTION. *Male*. Total length 3.88-4.56 (n=6). CL 1.80-2.3, CI 1.61-1.90. AL 1.92-2.2, AI 1.22-2.00, AH 1.40-2.24. Palp 2.72-2.88, leg I 11.84-16.52, leg II 7.12-10.60, leg III 4.04-5.92, leg IV 6.68-9.60. Leg formula 1243. Cymbium length ca. 0.8, width ca. 0.5.

Colour of carapace orange except for cephalic projection and area surrounding ALE and PLE (brown); sternum and palp orange, cymbium brown; legs brown, often orange on distal femora. Tarsi of leg IV pale yellow; abdomen as for female (see below), except lighter ventrally, silver dorsal pattern usually reduced to two pairs of lateral spots, and a black spot present posterior to base of spinnerets.

Abdomen triangular, dorsal tip not extending posterior to spinnerets.

*Female*. Total length 3.72-6.56 (n=11). CL 1.72-2.08, CI 1.41-1.73. AL 1.84-4.52, AI 1.09-1.48. AH 2.00-4.20. Palp 1.48-1.88, leg I 13.12-16.12, leg II 8.04-9.480, leg III 4.68-5.48, leg IV 7.68-8.80. Leg formula 1243. Epigyne width ca. 0.6.

Colour of carapace orange, dark brown around AME and between ALE and PLE; legs dark brown/black, except for base and for tarsi of leg IV (orange); palps and sternum orange; abdomen light grey-orange dorsally, large black spot on apex, four lateral silver patches near the posterio-dorsally, sometimes with two lateral silver spots anterio-dorsally (Fig. 4B); ventral abdomen brown. Colour of melanic specimens: abdomen black (with silver patches); carapace, palps and chelicerae orange-brown; sternum and legs dark brown, except for tarsus IV (pale yellow).

Carapace relatively wide (see CI). Abdomen conical/triangular, apex broad.

Egg sac chamber spherical, ca. 5.5 long, 5 wide; exit hole relatively narrow (Fig. 4D).

DISTRIBUTION AND ABUNDANCE. Japan (Chikuni, 1989), Australia (Rainbow, 1902, 1916), Amboina (Doleschall, 1857; Thorell, 1878), Papua New Guinea (Chrysanthus, 1963), India (Chrysanthus, 1963).

In eastern Australia, *A. miniaceus* is probably restricted to sub-tropical and tropical habitats, from Brisbane to the Torres Strait islands (Fig. 1A). Specimens have also been collected from coastal Northern Territory, as far west as Kemp Airstrip (12°35'S, 131°20'E). In southeast Queensland, I rarely found adults between May and October, but in tropical Queensland, the species appears common throughout the year. In southeast Queensland, this spider can be fairly abundant in rainforest pockets of North Stradbroke Island (27°28'S, 153°28'E). Melanic individuals can be found throughout the species range in Queensland.

REMARKS. Conspecificity of the Australian material with the juvenile female from NHMW was established by the overall shape and size. More accurate comparisons were made with the type of *A. walkeri* (synonymised by Berland, 1938) from AM. Several authors (including Chrysanthus, 1963) provide good illustrations of the epigyne, male carapace and palp. However,

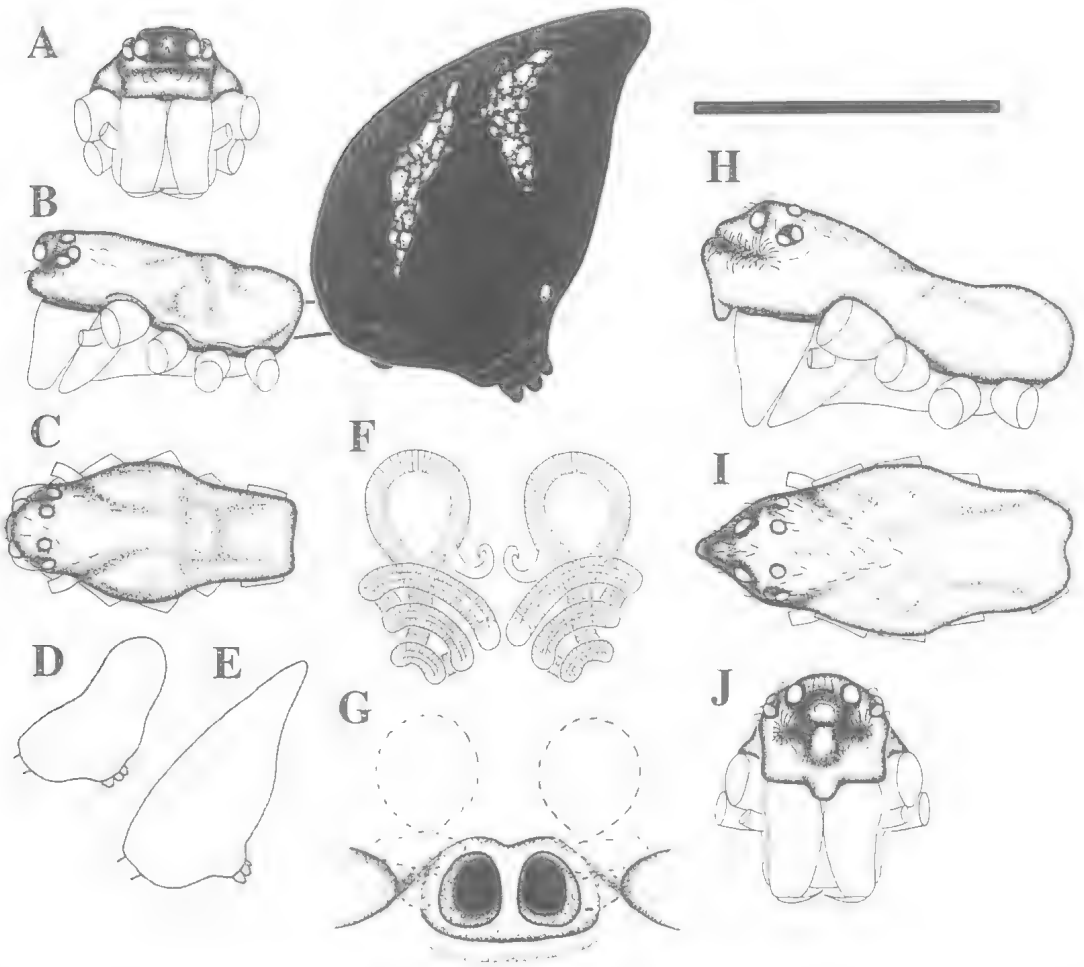



FIG. 5. *A. rainbowi*. A-C, female cephalothorax and abdomen; D, E, variation in shape of female abdomen; F, spermathecae and fertilisation ducts; G, epigyne; H-J, male cephalothorax. Scale bars: A-C, H-J = 1.2mm; D, E = 2.5mm; F, G = 0.320mm.

the descriptions in Thorell (1881: 161), Berland (1938: 162, figs 93, 94), Chen & Zhang (1991: 152, fig. 148.1-3), Chrysanthus (1975: 43) and Yaginuma (1978: 51, fig. 28.1) were insufficient to ascertain if their material is conspecific, and I did not examine their specimens.

### **Argyrodes rainbowi** (Roewer, 1942)
(Figs 2C, 5A-J)

*A. argentata* Rainbow, 1916: 50, pl. 15, fig. 24 (preoccupied by *A. argentata* Pickard-Cambridge, 1880).
*Argyrodina rainbowi* Roewer, 1942: 435. Replacement name for *A. argentata*.

MATERIAL. TYPE: *A. argentata* Rainbow, 1916, F, Gordonvale, Qld, Australia (AM). OTHER MATERIAL. New South Wales - AMKS18404, M, F, Blackbutt Reserve, Newcastle, 33°18'S, 151°19'E; AMKS18820, M, F, Reids Flat, Royal National Pk, 34°08'S, 151°04'E; AMKS44791, M, F, Calga, 33°25'S, 151°13'E; AMKS49163, M, F, North Ryde, 33°48'S, 151°06'E; AMKS49170, M, F, Pittwater, 33°38'S, 151°18'E; QMS29888, M, Cudgen, 28°16'S, 153°33'E; QMS29894, 3M, 2 F, Turners Dip, 31°01'S, 152°42'E; QMS46552, 3M, Sydney, 33°53'S, 151°13'E. Queensland - QMS29825, juv., QMS29826, M, QMS29827, F, QMS29828, M, Forty Mile Scrub, 18°05'S, 144°51'E; QMS29845, M, 2F, Mt Coolum, 26°34'S, 153°05'E; QMS29867, 2M, 2F, Lk Broadwater via Dalby, 27°21'S, 151°06'E; QMS29869, 2 M, F, Blackdown Tbld, via Dingo, 23°50'S, 149°03'E; QMS29870, M, 2F, Bundaberg Forest, 24°52'S, 152°21'E; QMS29881, M, 2F, Blue Lagoon area, Moreton I., 27°11'S, 153°24'E; QMS29889, F, Camp Milo, Cooloola, 26°00'S, 153°05'E; QMS29897, M, Coen, 13°56'S, 143°12'E; QMS29900, M, Black Mt, 16°39'S, 145°29'E; QMS29905, 2M, 2F, Davies Ck, 16°55'S, 145°32'E; QMS46498, M,

QMS46550, F, QMS46557, 3M, 2F, QMS46558, 2F, Pinkenba, 27°26'S, 153°07'E; QMS46499, M, QMS46506, M, QMS46539, M, QMS46541, F, QMS46543, F, QMS46555, 3M, 3F, Nathan, Brisbane, 27°33'S, 153°03'E; QMS46547, F, QMS46548, F, Chapel Hill, Brisbane, 27°28'S, 153°03'E; QMS46500, M, QMS46507, M, QMS46554, M, F, North Stradbroke I., 27°35'S, 153°27'E.

DIAGNOSIS. Male carapace and palp morphology are diagnostic. Unlike for remaining species (except *A. kulczynskii*, which appears closely related) cephalic and clypeal projections touch throughout their length (Fig. 5H-J), all eyes situated on cephalic projection, palpal embolus elongated and filiform (Fig. 2C). Lower frontal carapace, above base of chelicerae, with discrete ventrally-oriented notch (Fig. 5H,J) unlike *A. kulczynskii*, whose antero-ventral carapace is pointed and beak shaped. Also, base of embolus tear-shaped and almost globular for *A. kulczynskii* (Chrysanthus, 1963), but more angular and flat for *A. rainbowi* (Fig. 2C). *Argyrodes neocaledonicus* Berland, 1924 (albeit not recorded from Australia) is also similar in morphology and colour. However, male *A. neocaledonicus* has no notch on antero-ventral carapace and its cephalic projection is more rounded from dorsal aspect (Berland, 1924) than for *A. rainbowi*.

Epigyne small (see below) with oval, closely-spaced fossae, and shallow, oval indentations extending laterally from fossae (Fig. 5G). Unlike for remaining species (except *A. kulczynskii*), the insemination duct shows extensive coiling. However, insemination duct of *A. kulczynskii* is more coiled (5 times) than for *A. rainbowi* (3 times, Fig. 4F).

DESCRIPTION. *Male*. Total length 2.80-3.80 (n=12), CL 1.32-1.60, CI 1.81-2.06, AL 1.52-2.20, AI 1.36-2.29, AH 1.12-1.96, Palp 1.20-1.46, leg I 9.12-13.76, leg II 3.92-5.88, leg III 1.80-2.44, leg IV 2.64-3.64. Leg formula 1243. Cymbium length ca. 0.5, width ca. 0.3.

Colour of carapace, sternum, legs and abdomen as for female (see below); anterior latero-dorsal silver patch on abdomen often longer than posterior patch. In two specimens, a small, transverse, dull-silver band on ventral abdomen, between spinnerets and tip. Cymbium usually black.

Abdomen narrow, elongated, triangular, dorsal tip slightly behind spinnerets.

*Female*. Total length 2.36-3.80 (n=14). CL 1.08-1.28, CI 1.69-2.07, AL 1.32-2.40, AI 1.05-1.95, AH 1.48-3.00. Palp 0.76-0.96, leg I 6.60-8.88, leg II 2.76-3.72, leg III 1.40-1.72, leg IV 2.08-2.60. Leg formula 1243. Epigyne width ca. 0.3.

Colour of carapace, sternum and palps dark brown, legs sometimes lighter; abdomen black or dark brown, usually with two oblique, elongated, silver patches on each side (Fig. 5B). Shape and relative size of silver patches variable; anterior patches may extend ventrally to epigyne, or be interrupted, irregular, faded, or absent; sometimes, anterior and posterior patches form a continuous pattern. Two lateral, silver spots behind spinnerets, one central spot between spinnerets and epigyne, another central spot or short stripe (sometimes absent) behind abdominal apex.

Carapace relatively narrow (see CI). Abdomen usually tear drop-shaped (but shape may vary: Fig. 5D, E), apex usually extends slightly behind spinnerets (Fig. 5B).

Egg sac unknown.

DISTRIBUTION AND ABUNDANCE. Found throughout much of the eastern Australian coast, from warm, temperate habitats (e.g. Sydney, NSW) to tropical Queensland (Fig. 1B). In southeast Queensland, adults can be collected throughout the year.

REMARKS. Abdomen of the female type (=*A. argentatus*, Rainbow, 1916; AM) is slightly higher than that of most specimens that I examined. However, abdominal shape is quite variable for this and many other species of *Argyrodes* (Exline & Levi, 1962, figs 3D-E, 5D-E, 6J-K; pers. obs.). I could not distinguish the epigyne morphology of the type specimen from other examined *A. rainbowi*. Further, collection locality of the type (Gordonvale, 17°06'S, 145°47'E) is proximate to the geographic range of specimens that I examined (e.g. Forty Mile Scrub, 18°05'S, 144°51'E; QM).

Several specimens collected in far north Queensland (QM) closely resemble *A. rainbowi* except that the lower frontal part of the male carapace is straight, without a notch (see Diagnosis), and is not beak-shaped (*A. kulczynskii*). These resemble *A. neocaledonicus* (see Berland, 1924).

### **Argyrodes alannae** sp. nov.
(Figs 2D, 6A-K)

MATERIAL. HOLOTYPE: QMS35686, M, Nathan, Brisbane, Qld, 27°33'S, 153°03'E, Oct 95, P. Grostal, in dry sclerophyll forest, from web of *Cyrtophora moluccensis* Doleschall. OTHER MATERIAL: Victoria-

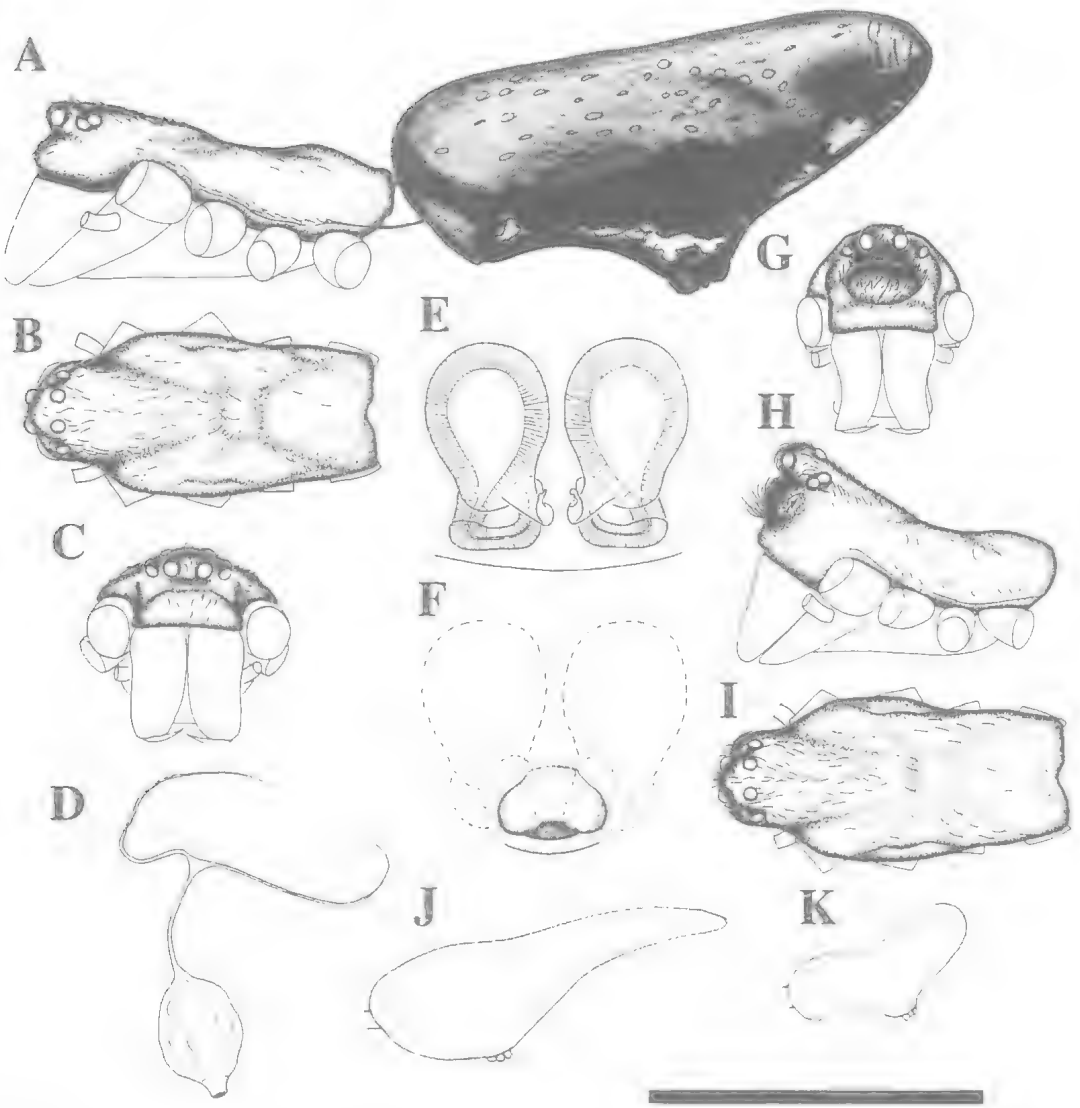



FIG. 6. *A. alannae* sp.nov. A-C, female cephalothorax and abdomen; D, egg sac; E, spermathecae and fertilisation ducts; F, epigyne; G-I, male cephalothorax; J, K, variation in shape of female abdomen. Scale bars A-C, G-I = 1.7mm; D = 21.4mm; E, F = 0.368mm; J, K = 12.6mm.

QMS35702, M, QMS35717, 2F, Edithvale. Tasmania - AMKS31178, M, Lindisfarne, 42°51'S, 147°21'E; AMKS31180, F, Opossum Bay, 42°59'S, 147°24'E; AMKS31346, M, juv., East Risdon, 42°50'S, 147°21'E; AMKS31347, M, F, Punch Bowl, 41°27'S, 147°10'E; AMKS31348, M, F, Trevallyn, Launceston, 41°27'S, 147°10'E. New South Wales - AMKS49164, M, F, Currawong, Broken Bay, 33°36'S, 151°18'E; AMKS49173, M, F, QMS35701, M, QMS35716, F, Sydney, 33° 53'S, 151° 13'E. Queensland - AMKS12820, F, Mt Dryander, via Prosperine, 20°15'S, 148°32'E; AMKS49162, F, Fraser I., 25°33'S, 152°59'E; QMS29838, M, Millstream Falls, 17°43'S, 145°26'E; QMS29843, F, QMS29863, 2F, QMS29882, M, F, Rochedale, Brisbane, 27°37'S, 153°09'E; QMS29853, 2M, 2F, Lk Nuga Nuga, 24°59'S, 148°40'E; QMS29857, M, F, juv., Koah Rd, 16°49'S, 145°31'E; QMS29858, 2F, 2 juv., Tinaroo, 17°10'S, 145°35'E; QMS29864, M, Wolfram, 17°05'S, 144°57'E; QMS29868, M, Blackdown Tbld, via Dingo, 23°50'S, 149°03'E; QMS29871, 2M, 2F, Bundaberg Forest, 24°52'S, 152°21'E; QMS29893, F, Homevale, 21°24'S, 148°33'E; QMS29898, M, 2F, Mt Garnet, 17°41'S, 145°07'E; QMS29903, 2M, 2F, Davies Ck, 16°55'S, 145°32'E; QMS29844, F, Mt Coolum, 26°34'S, 153°05'E; QMS35687, M, QMS35688, M, QMS35689, M,

QMS35690, M, QMS35691, M, QMS35692, M, QMS35693, M, QMS35697, M, QMS35698, M, QMS35699, M, QMS35703, F, QMS35704, F, QMS35705, F, QMS35706, F, QMS35707, F, QMS35708, F, QMS35710, F, QMS35712, F, QMS35714, F, QMS35715, F, Nathan, Brisbane, 27°33'S, 153°03'E; QMS35695, M, QMS35696, M, QMS35709, F, QMS35713, F, Chapel Hill, Brisbane, 27°28'S, 153°03'E; QMS35700, M, Gladstone, 23°51'S, 151°16'E; QMS35711, F, Pinkenba, Brisbane, 27°26'S, 153°07'E.

ETYMOLOGY. For Alanna.

DIAGNOSIS. Palp and cephalothorax of male *A. alannae* are diagnostic. Extension of median apophysis broad and tongue-like distally; embolus broad and evenly-tapering (Fig. 2D). Clypeal projection conspicuous, but shorter and broader relative to cephalic projection (Fig. 6G,H) than for remaining species (except for *A. fissifrons*). However, clypeal projection is pointed for *A. fissifrons* (Fig. 7H, I), but rounded for *A. alannae* (Fig 6G, H). ALE and PLE of *A. alannae* at base of cephalic projection (Fig. 6H), unlike for *A. antipodianus*, *A. miniaceus* or *A. rainbowi*. *Argyrodes wolfi* Strand (illustrated by Chrysanthus, 1975: 41, figs 160-164) also appears similar to *A. alannae* (see *A. fissifrons*: Diagnosis). However, for males, clypeal projection of *A. wolfi* is relatively long and parallel to cephalic projection; clypeal projection of *A. alannae* is shorter and distally diverging from cephalic projection (Fig. 6H). Female *A. alannae* can be separated by epigyne morphology. Gonopores of *A. alannae* are hidden under thick, trapezoid, upraised plate (Fig. 6F).

DESCRIPTION. *Male (Holotype)*. Total length 5.20. CL 1.82, CI 1.92. AL 3.46, AI 3.10, AH 1.24. Palp 2.42, leg I 11.50, leg II 7.60, leg III 4.10, leg IV 5.80. Leg formula 1243. Cymbium length ca. 0.8, width ca. 0.5.

Colour of cephalothorax dark brown, anterio-ventral part of cephalic projection almost black; palps and four proximal segments of leg I brown; otherwise, legs yellowish-brown, darker near patellae and tibial-metatarsal joints; cymbium dark brown. Abdomen dark grey, almost black, with two light spots on the posterior tip; laterally, a light line extending from spinnerets towards apex, then curving dorso-anteriorly, with several other light patches along latero-ventral surfaces; ventrally, longitudinal dark brown band with several light spots posteriorly; two parallel, longitudinal light patterns often extending latero-ventrally, joined by a posterio-ventral lateral crescent. Abdomen elongated, approx. triangular, with narrow, rounded apex; spinnerets horizontally half way between apex and pedicel.

*Other Males.* Often with dorsal, dull white spots on abdomen, less dense or prominent than for female. Abdominal apex is mobile and extendible, in some specimens appearing bulbous or slightly pointed (see below).

*Female*. Total length 5.09-8.04 (n=13). CL 1.53-2.04, CI 1.71-2.17. AL 3.27-6.83, AI 1.88-3.76, AH 1.02-2.84. Palp 1.24-1.67, leg I 9.16-13.59, leg II 5.89-8.51, leg III 3.48-4.94, leg IV 4.94-8.43. Leg formula 1243. Epigyne width ca. 0.2.

Colour of cephalothorax brown, darker around AME and around ALE and PLE. Chelicerae and palps brown (the latter sometimes yellowish); legs light yellowish-brown, darker near patellae and tibial-metatarsal joints; abdomen mostly reddish- or olive-brown; darker (almost black) latero-ventrally, towards apex, usually lined with a white patch pattern of variable shape and thickness (Fig. 6A); often, a small, oblique, white crescent towards abdominal tip; sometimes, abdominal colour more uniform and pattern less conspicuous; ventral abdomen reddish brown, often forming a wide longitudinal stripe with two or three curved transverse white lines posterior to spinnerets; many light speckles laterally and dorsally, either prominent or dull/inconspicuous (but always visible in fresh specimens).

Carapace relatively flat and elongated (see CI). Abdomen elongated, spinnerets often half way between pedicel and apex (Fig. 6A), their position variable depending on extension of abdomen. Abdomen (including the tip) may be long and fully extended (well fed or gravid females), or short, with a retracted tip (Fig. 6J,K). Apex mobile, sometimes curling anterio-dorsally. Medial part of abdomen dorso-ventrally flattened in several specimens (Fig. 6K).

Egg sac chamber large, urn-shaped, slightly elongated, ca. 9 long, 6 wide (Fig. 6D); exit hole relatively narrow.

DISTRIBUTION AND ABUNDANCE. This species has an extensive climatic range, occurring throughout the eastern Australian coast (Fig. 1B) from cool, temperate areas (e.g. Opossum Bay, Tasmania) to tropical Queensland (e.g. Davies Ck). In southeast Queensland, adults may be found throughout the year, but appear most numerous between October and May. Specimens from Tasmania, Melbourne and Sydney were also collected between these months.

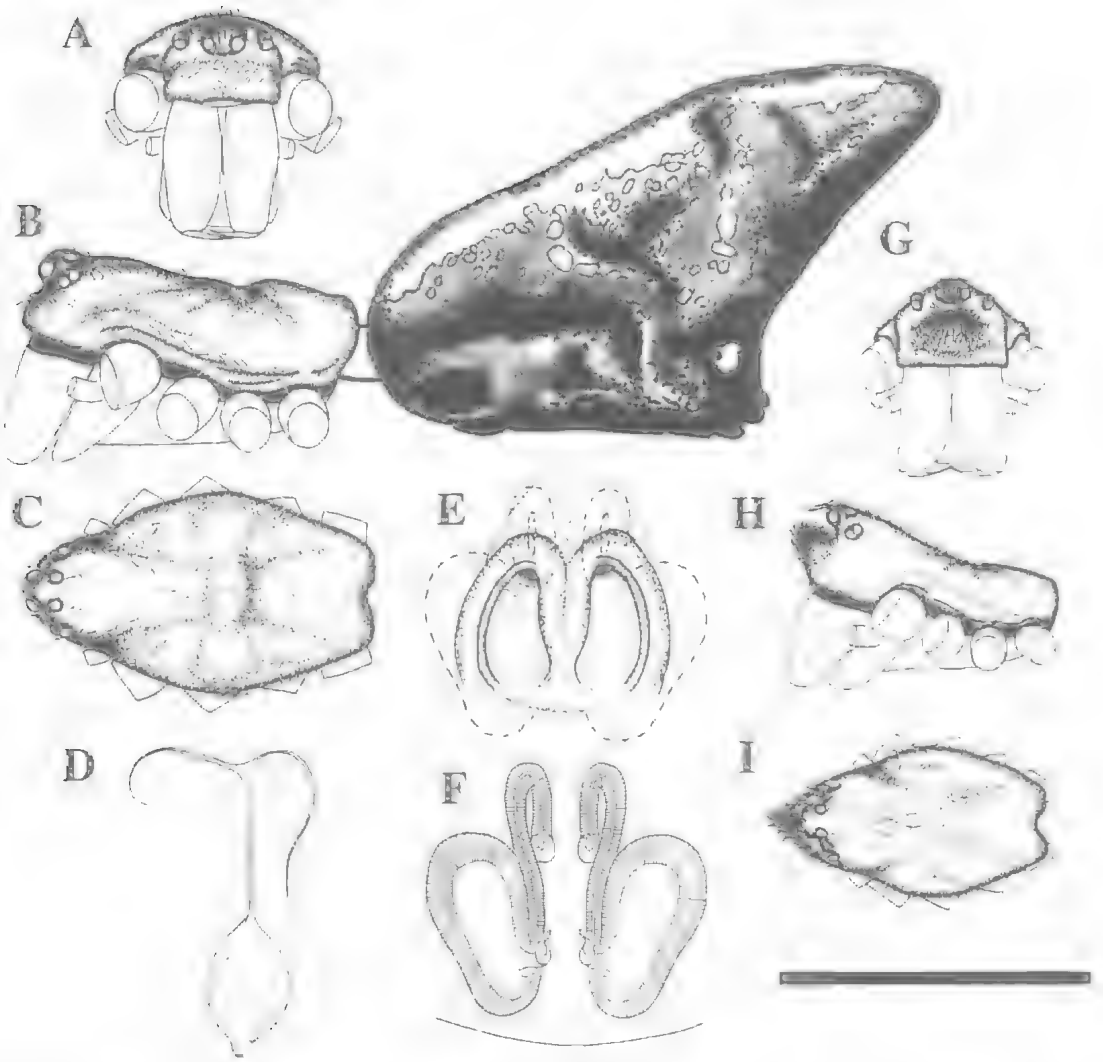



FIG. 7. *A. fissifrons*. A-C, female cephalothorax and abdomen; D, egg sac; E, spermathecae and fertilisation ducts; F, epigyne; G-I, male cephalothorax. Scale bars: A-C, G- I = 2.7mm; D = 24.9mm; E, F = 0.592mm.

**Argyrodes fissifrons**
Pickard-Cambridge, 1869
(Figs 2E, 7A-I)

*A. fissifrons* Pickard-Cambridge, 1869: 380, pl. 12, fig. 31-38; Thorell, 1878: 145; Pickard-Cambridge, 1880: 329, pl. 29, fig. 8a; Bonnet, 1957: 711; Chrysanthus, 1963: 737, figs 55-58; Levi et al., 1982: 106, fig. 1; Chikuni, 1989: 34, fig. 23; Platnick, 1991: 191.
*Argyrodina fissifrons* Roewer, 1942: 432.
*A. procrastinans* Pickard-Cambridge, 1880: 330, pl. 29, fig. 9 (first synonymised by Thorell, 1895).

MATERIAL. TYPE: *A. fissifrons* Pickard-Cambridge, 1869, (POSSIBLE TYPES, see Remarks), F's, egg sacs, Sri Lanka, leg. Thwaites (HEC). *A. procrastinans* Pickard-Cambridge, 1880, (POSSIBLE TYPE, see Remarks), F, Bombay, leg. Hobson (HEC). OTHER MATERIAL. HEC, F's, Amboina, 1878, leg. Thorell. Northern Territory - QMS29842, F, West Alligator R. mouth, 12°11'S, 132°16'E; QMS29852, M, F, juv., gorge NE of Mt Giltruth, 13°02'S, 133°05'E. Queensland - AMKS49155, F, Mossman, 16°28'S, 145°28'E; AMKS49157, M, Edmonton, 17°01'S, 145°45'E; AMKS49160, M, F, Wolfram, 17°05'S, 144°57'E; QMS29821, F, juv., QMS29832, M, QMS29833, F, QMS29835, F, Centenary Lks, Cairns, 16°55'S, 145°46'E; QMS29829, M, QMS29830, F, QMS46533, M, Cairns, 16°55'S, 145°46'E; QMS29841, F, Bundaberg Forest, 24°52'S, 152°21'E; QMS29849, 3M, F, Dulhunty R., 12°00'S, 142°07'E; QMS29851, F, Moreton I., 27°11'S, 153°24'E; QMS29854, M, F, Moreton I., 27°05'S, 153°26'E; QMS29856, M, Koah Rd, 16°49'S,

145°31'E; QMS29860, M, Kuranda, 16°49'S, 145°38'E; QMS29880, 2F, Mt Molloy, 16°41'S, 145°20'E; QMS29901, M, F, QMS29902, M, Black Mt., 16°39'S, 145°29'E; QMS46529, M, QMS46531, M, QMS46585, F, QMS46594, 3F, juv., Nathan, Brisbane, 27°33'S, 153°03'E; QMS46532, M, QMS46534, M, QMS46588, F, QMS46589, F, Pinkenba, 27°25'S, 153°07'E; QMS46535, M, QMS46579, F, Chapel Hill, Brisbane, 27°28'S, 153°03'E; QMS46595, 4F, juv., North Stradbroke I., 27°35'S, 153°27'E; QMS46596, F, juv., Yeppoon, 23°08'S, 150°45'E.

DIAGNOSIS. Males can be separated by cephalothorax and palp morphology. Unlike for other species, clypeal projection pointed, almost conical (Fig. 7G-I), cephalic projection with tuft of long, forward-pointing setae (Fig. 7H). ALE and PLE at base of cephalic projection, unlike for *A. antipodianus*, *A. miniaceus*, *A. rainbowi* and *A. kulczynskii*. Extension of median apophysis wide and curved distally; embolus narrow and short; conductor broad and flask-shaped (Fig. 2E). Female *A. fissifrons* are larger (>8.5mm body length) than females of remaining species (<8mm long). Large, reniform fossae (Fig. 7E) and long, u-shaped insemination ducts (Fig. 7F) are diagnostic for females.

A species similar to *A. fissifrons* (also resembling *A. wolfi* Strand) is found in north Queensland (QM), but clypeal projection of males is rounded, not pointed. For females, epigyne is much smaller than for *A. fissifrons*, with round (not reniform) fossae.

DESCRIPTION. *Male.* Total length 4.94-6.83 (n=8). CL 1.82-3.13, CI 1.67-1.83. AL 2.55-3.85, AI 2.00-2.56, AH 1.31-2.47. Palp 3.49-4.65, leg I 14.76-24.43, leg II 9.31-15.99, leg III 5.38-9.31, leg IV 9.16-15.56. Leg formula 12(=)43 (relative lengths of legs 2 and 4 may vary slightly, but are approximately equal in almost all specimens that I examined). Cymbium length ca. 0.8, width ca. 0.5.

Colour of cephalothorax, palps and legs orange/orange-brown. Legs sometimes darker near patellae and towards distal sections of tibiae. Abdomen grey-orange to brown, with silver speckling (but less numerous than for female). Transverse or oblique curved patterns formed by silver speckling and brown patches. Often two lateral light spots posterior to spinnerets, sometimes inconspicuous on shrunk or lightly coloured abdomens. Abdomen shape similar to that of female (see below).

*Female.* Total length 8.51-11.34 (n=12). CL 2.55-3.34, CI 1.60-1.83. AL 5.31-7.99, AI 1.70-2.81, AH 2.69-5.31. Palp 2.04-2.55, leg I 21.74-27.34, leg II 14.54-17.74, leg III 8.94-10.25, leg IV 16.14-19.48. Leg formula 1423. Epigyne width ca. 0.7.

Colour of cephalothorax orange to orange-brown, darker around ALE and PLE; palps and legs as for male. Abdomen from grey-orange, to orange and brown, darker ventrally; relatively dense, conspicuous speckling of silver spots (esp. dorsally), forming long, curving patterns laterally. Often, dark brown, elongated patterns on lateral sections of abdomen (Fig. 7B). Ventrally, posterior to spinnerets, two large, lateral light spots with dark perimeter.

Abdomen elongated, extending beyond spinnerets, but relatively wide and high (Fig. 7B); central part may be dorso-ventrally flattened. Two lateral thickenings near apex. Tip often pointed, but as for *A. alannae* (Fig. 6J), it may be retracted and appear bulbous; apex probably not mobile, as it was not curled for any of the examined specimens (see *A. alannae*). Spinnerets about half way between pedicel and apex; position less variable than for *A. alannae* (Fig. 6J,K). Epigyne oval, well sclerotised.

Egg sac as for *A. alannae* (Fig. 6D), but slightly larger ca. 11 long, 7 wide (Fig. 7D).

DISTRIBUTION AND ABUNDANCE. Amboina (Pickard-Cambridge, 1880), Sri Lanka (Pickard-Cambridge, 1869; 1880), Japan (Chikuni, 1989), Papua New Guinea (Levi et al., 1982).

In eastern Australia, specimens were taken throughout subtropical and tropical coastal regions (Fig. 1B), from Brisbane to Dulhunty R. (north Qld). The species has also been collected from coastal Northern Territory (e.g. Mt Gilruth). In southeast Queensland, I collected adults between December and May, while specimens from tropical regions were collected throughout the year.

REMARKS. The present location of the types of *A. fissifrons* is in doubt. Chrysanthus (1963, 1975) and Levi et al. (1982) noted that the type is in the Natural History Museum (London), but P. Hillyard (curator) did not locate it there. I am uncertain if the examined Sri Lankan specimens from HEC include the type of *A. fissifrons*. The material consists of a series of adults and egg sacs, (as in original description) but the collector name (Thwaites) is different from that in the original description (Nietner). Possibly, the collector details are a lapsus by Pickard-Cambridge (I. Lansbury, pers. comm.).

Conspecificity was established between the specimens from Queensland and Pickard-Cambridge's material from Sri Lanka and Amboina on the basis of palp and carapace morphology of males, and by the epigyne. I could not establish a difference between the specimen of *A. procrastinans* from Bombay (HEC) and my material (although the holotype of *A. procrastinans* is not designated, the sex (F), locality and collector details (J. Hobson) of the specimen agree with the original description).

Previous publications show contrasting illustrations of *A. fissifrons*. Illustrations by Chrysanthus (1975: 41, figs 156-159) of epigynes from Papua New Guinea material show insemination ducts that are wider (relative to spermathecae) and shorter than those of the specimens described here. The drawing of the epigyne of *A. fissifrons* by Levi et al. (1982) shows relatively short, simple insemination ducts. The authors did not provide a description of their material, except for comments on the resinous accretion covering the epigyne. Illustrations provided by Feng (1990: 90, figs 1-5) show the insemination ducts following a zig-zag, rather than a U-shaped (Fig. 7F) path. Further, the fossae illustrated by Feng are directed towards each other (forming a heart-shape), rather than being parallel. Thorell (1895: 117) and Yaginuma (1978: 32, pl. 6, fig. 30) did not provide sufficient information to establish conspecificity and I did not examine their material.

ECOLOGY AND BEHAVIOUR. Behaviourally, *Argyrodes* is a diverse genus, and some species (e.g. *A. colubrinus*) are probably not kleptobiotic (Clyne, 1979; Eberhard, 1979; Mascord, 1980; Elgar, 1993; pers. obs.). In contrast, other species seem highly adapted to a kleptobiotic lifestyle. *Argyrodes antipodianus* can remove prey from host webs using complex techniques that include attaching its own silk threads to a prey item, cutting the prey from the web and swinging with the stolen item away from the host's orb: a behaviour aptly named the 'Tarzan swing' (Whitehouse, 1986). This inquiline can steal prey over 30 times heavier than its own body weight, within less than 20 seconds (pers. obs.). The spider can also feed, apparently undetected, on items that are simultaneously consumed by the host (Whitehouse, 1988). Foraging behaviour of kleptobiotic *Argyrodes* may also depend on the host to kleptobiont size ratio (see Larcher & Wise, 1985). Stealthy food theft may be difficult for relatively large and heavy spiders (e.g. *A. fissifrons*), and the level of direct interaction with the host may increase for these species (Elgar, 1993).

Several species of kleptobiotic *Argyrodes* have been called commensals (Kaston, 1965; Exline & Levi, 1962; Wise, 1982; Bradoo, 1983), as they were thought to remove prey that was small and of little interest to the host. If so, referring to these spiders as 'klepto-parasites' would not be justified (Vollrath, 1984). However, some species (e.g. *A. antipodianus*) can also remove large prey items, otherwise consumed by the host (Whitehouse, 1986; pers. obs.). Negative effects of foraging by kleptobiotic *Argyrodes* are strongly supported by the fact that some species such as *A. antipodianus* can reduce their host's weight gain (Grostal & Walter, 1997). Apart from stealing food, several *Argyrodes* species may consume their host's web (Vollrath, 1987; Shinkai, 1988; Whitehouse, 1986; Grostal & Walter, 1997), itself a nutritious resource (Peakall, 1971; Higgins, 1987; Townley & Tillinghast, 1988; Sherman, 1994). Also, some kleptobionts, including *A. antipodianus* can facultatively prey on the host, especially when the latter is moulting (Lubin, 1974; Smith Trail, 1981; Wise, 1982; Tanaka, 1984; Whitehouse, 1986, 1987; Elgar, 1993).

The degree of colonisation of webs by *Argyrodes* may be determined by the characteristics of these webs. Some webs are frequently colonised, while others rarely, if ever, contain the kleptobionts (Levy, 1985; Whitehouse, 1988; Grostal & Walter, in press). Perhaps some webs may be easier to forage on, or may catch more food (Whitehouse, 1988; Elgar, 1989). Furthermore, host specificity among species of kleptobiotic *Argyrodes* appears to differ. Some species are found on webs of many spiders, while others appear restricted to a narrow range of hosts (Elgar, 1993; pers. obs.). For example, *A. antipodianus* can be found on webs of a wide variety of spiders (Table 1). In contrast, *A. fissifrons* was previously collected from hosts from four families, but in east Queensland I recorded this kleptobiont only from webs of *Cyrtophora* species, even in areas where other potential hosts (e.g. *Nephila* spp.) are more numerous. Reasons for the apparent restriction in host range among different species of *Argyrodes* are still unclear. Perhaps, some species of *Argyrodes* are less efficient at dispersal between webs than others, and are thus restricted to webs that have a high longevity. Also, large and relatively slow-moving

TABLE 1. Host records of five species of kleptobiotic *Argyrodes* from southeast Queensland. * original source taken from Elgar, 1993.

| Argyrodes species | Host species (family) | Source |
|---|---|---|
| *A. antipodianus* | *Cambridgea* sp. (Agelenidae) | Whitehouse 1988* |
| | *Badumna longiqua* (Amaurobidae) | Whitehouse 1988* |
| | *Araneus dimidiatus* (Araneidae) | P. Grostal, pers. obs. |
| | *Argiope* sp. (Araneidae) | P. Grostal, pers. obs. |
| | *Cyclosa trilobata* (Araneidae) | Whitehouse 1988* |
| | *Cyrtophora hirta* (Araneidae) | Elgar et al. 1983, P. Grostal, pers. obs. |
| | *Cyrtophora moluccensis* (Araneidae) | P. Grostal, pers. obs. |
| | *Cyrtophora* sp. (Araneidae) | P. Grostal, pers. obs. |
| | *Eriophora crassa* (Araneidae) | Whitehouse 1988* |
| | *Eriophora pustulosa* (Araneidae) | Whitehouse 1988* |
| | *Eriophora transmarina* (Araneidae) | P. Grostal, pers. obs. |
| | *Gasteracantha* sp. (Araneidae) | P. Grostal, pers. obs. |
| | *Pholcus phalangioides* (Pholcidae) | Whitehouse 1988* |
| | *Stiphidion* sp. (Stiphidiidae) | Whitehouse 1988* |
| | *Leucauge dromedaria* (Tetragnathidae) | Whitehouse 1988* |
| | *Nephila edulis* (Tetragnathidae) | Elgar 1989* |
| | *Nephila pilipes* (Tetragnathidae) | P. Grostal, pers. obs. |
| | *Nephila plumipes* (Tetragnathidae) | P. Grostal, pers. obs. |
| | *Nephilengys* sp. (Tetragnathidae) | P. Grostal, pers. obs. |
| | *Phonognatha graeffei* (Tetragnathidae) | P. Grostal, pers. obs. |
| | *Achearanea* (Theridiidae) | Whitehouse 1988* |
| | *Latrodectus geometricus* (Theridiidae) | P. Grostal, pers. obs. |
| *A. rainbowi* | *Araneus dimidiatus* (Araneidae) | P. Grostal, pers. obs., |
| | *Argiope* sp. (Araneidae) | P. Grostal, pers. obs. |
| | *Cyrtophora hirta* (Araneidae) | P. Grostal, pers. obs. |
| | *Cyrtophora moluccensis* (Araneidae) | P. Grostal, pers. obs. |
| | *Eriophora transmarina* (Araneidae) | P. Grostal, pers. obs. |
| | *Nephila plumipes* (Tetragnathidae) | P. Grostal, pers. obs. |
| | *Phonognatha graeffei* (Tetragnathidae) | P. Grostal, pers. obs. |
| *A. miniaceus* | *Argiope* sp. (Araneidae) | P. Grostal, pers. obs. |
| | *Nephila pilipes* (Tetragnathidae) | Robinson & Robinson 1973*, P. Grostal, pers. obs. |
| | *Nephila plumipes* (Tetragnathidae) | P. Grostal, pers. obs. |
| | *Nephilengys* sp. (Tetragnathidae) | P. Grostal, pers. obs. |
| *A. alannae* | *Cyrtophora hirta* (Araneidae) | P. Grostal, pers. obs. |
| | *Cyrtophora moluccensis* (Araneidae) | P. Grostal, pers. obs. |
| | unidentified sp. (Pholcidae) | P. Grostal, pers. obs. |
| | *Nephila plumipes* (Tetragnathidae) | P. Grostal, pers. obs. |
| | *Phonognatha graeffei* (Tetragnathidae) | P. Grostal, pers. obs. |
| | *Achearanea* sp. (Theridiidae) | P. Grostal, pers. obs. |
| *A. fissifrons* | *Agelena limbata* (Agelenidae) | Tanaka 1984* |
| | *Cyrtophora hirta* (Araneidae) | P. Grostal, pers. obs. |
| | *Cyrtophora moluccensis* (Araneidae) | P. Grostal, pers. obs. |
| | *Cyrtophora* sp. (Araneidae) | P. Grostal, pers. obs. |
| | *Linyphia* sp. (Linyphiidae) | Tanaka 1984* |
| | *Theridion japonicum* (Theridiidae) | Tanaka 1984* |
| | *Philoponella* sp. (Uloboridae) | Elgar 1993 |
| | *Uloborus varians* (Uloboridae) | Tanaka 1984* |

kleptobionts such as *A. fissifrons* may be most successful on webs that have a sturdy construction (e.g. *Cyrtophora moluccensis*; pers. obs.), while the relatively small *A. antipodianus* (Whitehouse & Jackson, 1993) may successfully forage on smaller, more delicate webs (e.g. *Argiope* spp., pers. obs.).

Habitat requirements may also vary for different species of *Argyrodes*. For example, *A. antipodianus*, *A. rainbowi, A alannae* and *A. fissifrons* may be found in a wide range of habitats, from open, dry sclerophyll forest to rainforest. *A. antipodianus* may be found in dry, rocky areas with almost no vegetation cover (Kabra, near Rockhampton, 23°22'S, 150°31'E). This species may be more tolerant to sun exposure because of the silver colour of its abdomen (Robinson & Robinson, 1978; Vollrath, 1987). In contrast, I collected *A. miniaceus* only from wet, shaded habitats, e.g. near creeks or along edges of rainforest, although many of this spider's hosts (e.g. *Nephila plumipes*) are common in drier areas.

Relative abundance on host webs differs among species of the kleptobionts. When I surveyed webs of *Nephila edulis* in southeast Queensland, I found an average of 4.47 (± .59 SE) *A. antipodianus* (n=51) with up to 25 individuals per web. *A. miniaceus* can also be numerous: I collected up to 20 of these inquilines from webs of *N. pilipes* (Linnaeus) (usually referred to as *N. maculata*). However, abundance of *A. alannae* and *A. fissifrons* is usually limited to less than five individuals per host web. Of 161 webs of *C. moluccensis* that I observed in eastern Queensland, I found an average of 0.73 (± .09 SE) *A. fissifrons* per web.

The ecology of kleptobiotic *Argyrodes* and their interaction with host spiders is fascinating and complex, and needs to be studied in greater depth. Topics of special interest include the factors that determine the abundance and distribution of *Argyrodes* on host webs, the intrageneric variation in behaviour of the kleptobionts, and the effects of these spiders on host fitness. However, ecological and behavioural studies of these unique spiders should be first validated by a sound taxonomic knowledge of the observed species.

## ACKNOWLEDGEMENTS

I thank David Walter and Robert Raven for their extensive help in all aspects of this study, Val Davies for all her advice and Phil Lawless for his assistance with data and specimen retrieval. Also, Rebecca Harris, Mike Gray and Graham Milledge (AM), Ken Walker (Museum of Victoria), Ivor Lansbury, Malgosia Atkinson (HEC), Jürgen Gruber (NHMW) for their help and loans of material, as well as Margaret Schneider and Paul Hillyard for their assistance with specimen location. Doug Wallace provided enthusiastic help with accommodation and specimen collection in Rockhampton and Yeppoon. Val Davies, Norman Platnick and Mary Whitehouse provided many useful suggestions that improved the manuscript. The research was partly sponsored by the Australian Postgraduate Award, Department of Entomology (University of Queensland) and the Queensland Museum.

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# REVISION OF *TYPOSTOLA* SIMON (ARANEAE: HETEROPODIDAE) IN AUSTRALASIA

DAVID B. HIRST

Hirst, D.B. 1999 06 30: Revision of *Typostola* Simon (Araneae: Heteropodidae) in Australasia. *Memoirs of the Queensland Museum* **43**(2): 639-648. Brisbane. ISSN 0079-8835.

*Typostola* Simon and its type *T. barbata* (L. Koch) are revised. *T. broomi* Hogg, *T. magnifica* Hogg and *T. major* Hogg are synonymised with *T. barbata*. *T. heterochroma*, *T. pilbara* and *T. tari* are described as new. ❐ *Araneae, Heteropodidae, Typostola, revision, new taxa.*

*David B. Hirst, South Australian Museum, North Terrace, Adelaide 5000, Australia; 15 September, 1998.*

*Typostola* Simon, 1897 was erected for *Isopeda barbata* L. Koch, 1875 which possessed a unique setal fringe on the inner edge of the chelicera. *T. broomi*, *T. magnifica* and *T. major*, were described by Hogg (1902). Järvi (1912) transferred *T. magnifica* to *Zachria* L. Koch on the basis of the female genitalia. Hirst (1991) returned *magnifica* to *Typostola*.

Hogg (1902) noted that differences between *T. broomi*, *T. magnifica* and *T. major* are minor. All are considered synonyms of *T. barbata*. The genus can be divided into two groups with *T. barbata* and *T. tari* comprising one group and *T. heterochroma* and *T. pilbara* the second, the latter having a more derived male embolus and female vulva. Although lacking a cheliceral setal fringe, all new species share with *T. barbata* the same structure in the genitalia, eye arrangement and leg indices.

## METHODS

Materials and methods are as in Hirst, 1991. Types of newly described species are deposited in Australian museums. All measurements are in millimetres.

ABBREVIATIONS. *Institutions*. AM, Australian Museum, Sydney; BMNH, British Museum of Natural History , London; HNHM, Hungarian Natural History Museum; MMUS, Macleay Museum, University of Sydney; MNHP, Museum National D'Histoire, Paris; MV, Museum of Victoria, Melbourne; NHMW, Naturhistorisches Museum, Wien; NHRM, Naturhistoriske Riksmuseum, Stockholm; QM, Queensland Museum, Brisbane; SAMA, South Australian Museum, Adelaide; SMF, Natur-Museum Senckenburg, Frankfurt; ZMB, Museum Humboldt Universität, Berlin; ZMH, Zoologisches Museum, Hamburg; WAM, Western Australian Museum, Perth.

*Other Abbreviations*. AL, abdomen length; AW, abdomen width; aw, anterior width; CL, carapace length; CW, carapace width; L, or l, length; MOQ, median ocular quadrangle; NSW, New South Wales; NT, Northern Territory; PNG, Papua New Guinea; pw, posterior width; Qld, Queensland; WA, Western Australia; W, or w, width. Other abbreviations are standard for the Araneae.

## SYSTEMATICS

### **Typostola** Simon, 1897

*Isopeda* (part) L. Koch, 1875: 680.
*Typostola* Simon, 1987: 44; Hogg, 1902: 423, 455; Simon, 1903: 1021; Roewer, 1954: 682; Bonnet, 1959: 4748; Hirst, 1991: 5.
*Zachria* (part): Järvi, 1912: 90; 1914: 218.

Type species *Isopeda barbata* L. Koch, 1875 by original designation.

DIAGNOSIS. Carapace longer than wide, low, convex. Chelicera with or without setal fringe. Sternum longer than wide. Legs I, II of females 4-5 times carapace length. Female spermathecal sacs tubular, long, looped to anterior. Palpal tibial apophysis of known males relatively short with robust membraneous support, embolus coiled 1¾ -3½ times in distal half of cymbium; median apophysis convex, subcontiguous or contiguous with base of conductor.

DESCRIPTION. Large spiders. Carapace longer than wide, low, 3-4 times longer than high, convex, gently rounded sides, flattish medially, highest anterior of fovea (Fig. 1A); fovea a discernible shallow groove; surrounding area not depressed. ALE usually largest, sometimes AME largest; distance between AME equal to or

greater than between AME-ALE; anterior row, from above, slightly procurved, posterior row slightly recurved. Chelicerae with 2 promarginal teeth; usually 5 retromarginal teeth, occasionally 4 or 6 on one chelicera, rarely on both, distal teeth subequal (Fig. 3C) occasionally distal tooth largest (Fig. 4F); plumose setae present as dense setal fringe on prodorsal face of chelicera (Fig. 1B) or absent. Maxillae with or without dense long plumose setae retrolaterally. Palpal trochanter, femora and tarsi may have plumose setae ventrally. Labium wider than long. Sternum longer than wide, widest mid-length; may have dense white or yellow setae on margins. Legs relatively long, legs I, II of females 4-5 times length of carapace, of males 5 to >6 times. Leg I when outstretched alongside leg II reaches to or near base of tarsi II, never beyond. Abdomen longer than wide, rounded, without pattern, but may have median spots or posterior chevrons (Fig. 4D), venter without pattern or with dark stripes (Fig. 3E) or brown badge (Fig. 4E). Palpal tibial apophysis of known males relatively short and thick with robust membraneous support, embolus coiled 1¾–3½ times alongside lesser coiled conductor in distal half of cymbium; median apophysis convex, rounded and subcontiguous or narrow and contiguous with conductor. Female epigynum large, occupying 3/5 distance between epigastric furrow and pedicel; width of sclerotisation lateral to fossa equals width of fossa, outer margin of sclerotisation defined; fossa deeply recessed anteriorly, whitish, but posterior margin pigmented. Spermathecal sacs tubular, long, curved and reaching to beyond anterior of insemination ducts (Figs 4B, 5A) occasionally further recurved to follow insemination ducts (Fig. 1E).

REMARKS. Male *Typostola* have a low embolic coil number compared with the insemination duct coil number of the female where both sexes are known. However, it shares this character with *Eodelena* Hogg and *Zachria* the only other Deleninae genera so far revised in which the female has a greater number of coils. *Typostola* is most similar to *Zachria* from which it is separated by having relatively longer legs, convex carapace and the short thick male palpal tibial apophysis. The male palp of *Typostola* also resembles that of *Eodelena* but the latter has an acuminate or obtuse apex on the median apophysis (Hirst, 1991) while female *Eodelena* lack spermathecal sacs. Although similar in leg indices, *Eodelena* further differs in having a low flattish, wider than long carapace. Unlike *Zachria* and *Eodelena* which are medium to small heteropodids having a southern Australian distribution, *Typostola* are large and found in northern Australia and New Guinea. Little is known of their habits but personal observations indicate they may prefer to frequent the upper trunk or branches of trees.

## KEY TO SPECIES OF *TYPOSTOLA* SIMON

FEMALES

1. Chelicera without setal fringe on inner edge; insemination ducts with 4¼-4½ coils; spermathecal sacs reach to anterior of fossa (Figs 4B, 5A) not recurved . . . . . 2
   Chelicera with setal fringe on inner edge; insemination ducts with 2½ coils; spermathecal sacs further recurved to follow fertilisation ducts (Fig. 1E) . . . . *T. barbata* (L. Koch)
2. Fossa lacks cavities anteriorly (Fig. 4A); dorsal abdomen with posterior chevron markings, venter brown . . . . . *P. heterochroma*, sp. nov.
   Fossa with pair of cavities anteriorly (Fig. 5A); abdomen without pattern . . . . . *T. pilbara*, sp. nov.

MALES

1. Chelicera without setal fringe on inner edge . . . . . 2
   Chelicera with setal fringe on inner edge . . . . . *T. barbata* (L. Koch)
2. Abdomen without dorsal pattern; median apophysis oval (Fig. 3D); embolus with 2 coils . . . . . *T. tari*, sp. nov.
   Abdomen with dorsal pattern (Fig. 4D); median apophysis elongate (Fig. 4I); embolus with 3½ coils . . . . . *T. heterochroma*, sp. nov.

### **Typostola barbata** (L. Koch)
(Figs 1,6; Table 1)

*Isopeda barbata* L. Koch, 1875: 680, plate 56, fig. 3.
*Typostola barbata*: Simon, 1897: 44.
*Typostola broomi* Hogg, 1902: 455, fig. 100. New synonymy.
*Typostola magnifica* Hogg, 1902: 457, fig. 101; Hirst, 1991:5. New synonymy.
*Typostola major* Hogg, 1902: 459. New synonymy.
*Zachria magnifica*: Järvi, 1912: 90, pl. 9, figs 9, 10.

MATERIAL. SYNTYPES: The series from Port Mackay and Sydney contains at least two specimens one of which was a female. Whereabouts of syntypes unknown. OTHER MATERIAL. New South Wales: SAMAN1994208, F, Warialda, 29°32'S 150°35'E. Queensland: BMNH 1898.11.7.3 Holotype male of *Typostola broomi*, Muldiva, 17°13'S 144°29'E; BMNH1898.11.7.4, syntype female of *Typostola magnifica*; BMNH1893.3.23.1, holotype F of *Typostola major*, Queensland; QMS21690, M, Allingham Creek, 19°45'S 145°41'E; QMS14136, F, Alton, 27°55'S 149°43'E; QMW229, F, Auchenflower, Brisbane, 27°28'S 153°01'E; QMS21681, F, Bald Hills, Brisbane; QMS6910, F, Beaudesert, 27°59'S 153°00'E; QMS21696, F, Booubyjan, 25°57'S 151°55'E; QMS21694, F, Bracken Ridge, Brisbane; QMS21691, juv., Brookfield, Brisbane; QMS14135, F, Callide Power Stn, Biloela, 24°24'S

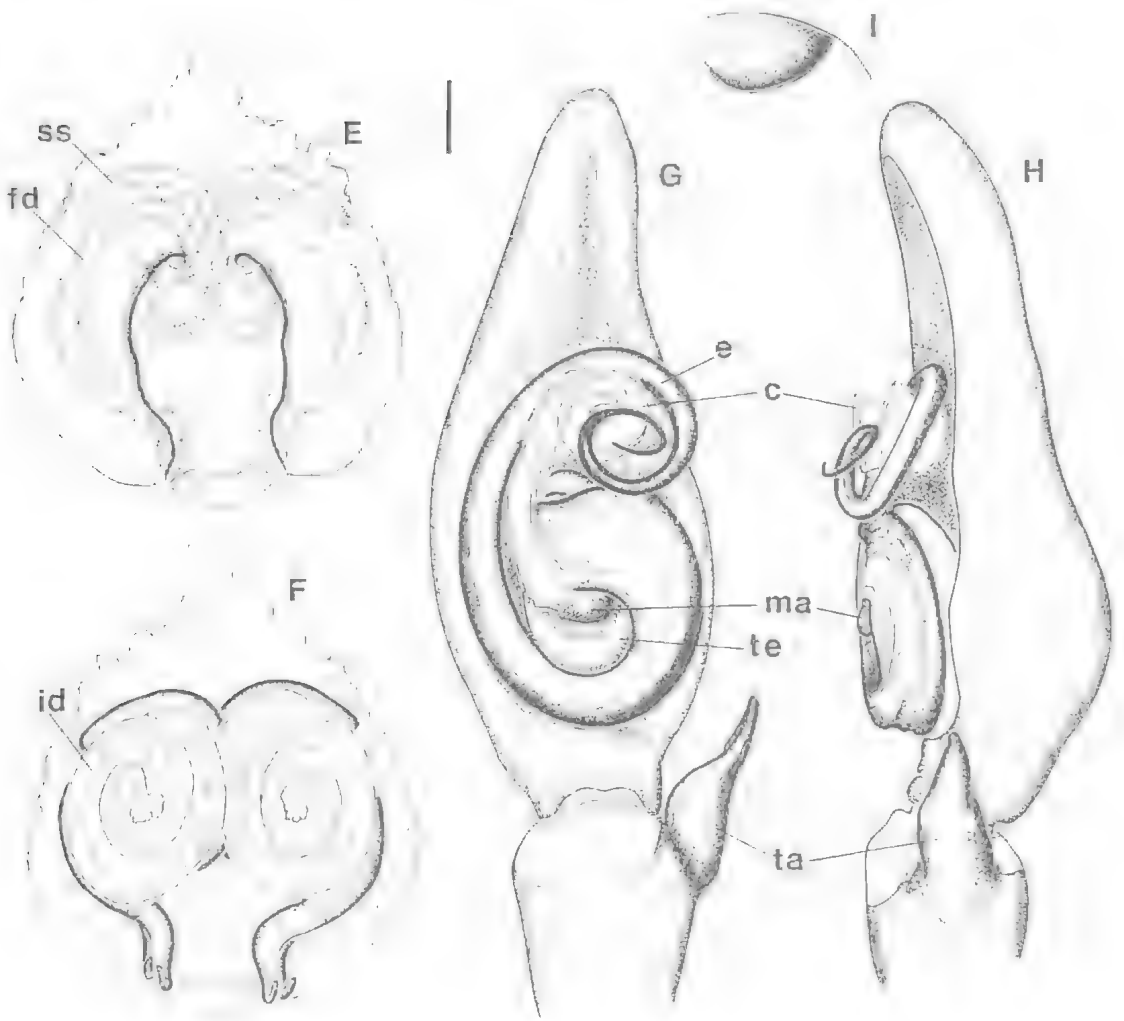



FIG. 1. *Typostola barbata* (L. Koch). A-E, F, A, carapace, lateral; B, chelicerae and ocular area; C, epigynum of holotype *T. magnifica*; D, ditto of *T. major*; E, F, epigynum of SAMAN1994208, E, ventral, cleared; F, dorsal. G-I, male. G, H, left palp of holotype *T. broomi*, G, ventral, H, retrolateral; I, median apophysis of QMS21677. Scale bars; A, B, 1mm, C-H, 0.5mm, I, not to scale. c = conductor; e = embolus; fd = fertilisation duct; id = insemination duct; ma = median apophysis; ss = spermathecal sac; ta = tibial apophysis; te = tegulum.

150°31'E; QMS21671, F, Caloundra, 26°48'S 153°08'E; QMS21688, juv., Camira, Brisbane; QMS21685, penult. F, Camp Hill, Brisbane; QMS21689, juv., Carnarvon Lodge, 24°50'S 147°45'E; QMS14141, F, Chinchilla, 26°44'S 150°38'E; QMS17683, F, Coominya, 27°24'S 152°30'E; QMS21678, F, Cooparoo, Brisbane; QMW533, F, Corinda, Brisbane; QMD10700, F, Eidsvold, 25°22'S 151°07'E; QMW1629, F, juv., Einasleigh, 18°31'S 144°05'E; W1147, W1148, penult. F, juv., Enoggera, Brisbane; QMS21692, M, Fortitude Valley, Brisbane; QMS21667, F, Gatton, 27°34'S 152°17'E; QMS21684, penult. F, Goodna, Brisbane; QMS21673, S21687, 2 juv., Goondiwindi, 28°33'S 150°18'E; QMS14137, F, Jandowae, 26°47'S 151°07'E; QMS21693, M, Lk Broadwater, 27°21'S 151°06'E; QMS21697, F, Leichardt, 23°03'S 144°54'E; QMS14139, F, Moonie, 27°43'S 150°22'E; QMS21670, M, Mt Gravatt, Brisbane: QMS14140, F, Mt Isa, 20°44'S 139°29'E; QMS14465, juv., Mt Moffat, 25°01'S 147°57'E; QMS21676, F, Mt Molloy, 16°41'S 145°20'E; QMW496, F, M, Mt Pleasant, 27°09'S 152°46'E; QMS21675, F, Nangram Lagoon, 26°50'S150°17'E; QMS21695, F, Narangba, 27°12'S 152°58'E; QMS21677, M, New Farm, Brisbane; QMS14138, F, Rockhampton, 23°22'S 150°32'E; MNHP No. 1688, F, same locality; QMS21674, S21682, 2M, Rosewood, Brisbane; QMS21686, W148, 2 F, Samford, Brisbane; QMS21680, F, St Lucia, Brisbane;

QMS21672, F, Thornlands, Brisbane; QMS21683, juv., Toogoolawah, 27°05'S 152°23'E; QMS21679, F, Victoria Barracks, Brisbane; QMS21668, QMS21669, 2 F, no data; SAMAN1994209, F, no data.

DIAGNOSIS. Colour yellow-brown. ALE largest. Dense plumose setae on inner edge of chelicera, retrolateral maxillae, and ventrally on palpal trochanter, femora and tarsi. Male palpal tibial apophysis relatively short, blunt; median apophysis small; embolus with 1¾-2 coils apically. Female spermathecal sacs long, arced anteriorly then recurved to posterior adjacent each fertilisation duct; insemination ducts with 2½ lightly sclerotised coils.

DESCRIPTION. Female (holotype *T. major*): CL 15.8, CW 14.5. AL 17.8, AW 12.5.

*Colour in alcohol.* As in Hogg (1902); carapace red-brown, caput dark brown in ocular area. Upright setae yellow-brown, adpressed setae yellow-white. Chelicerae black-brown. Maxillae and labium red-brown. Sternum orange-brown. Coxae I orange-brown, dense yellow setae. Legs red-brown. Abdomen brown with pair of median black spots.

*Eyes.* AME 0.84. AME:ALE:PME:PLE 1: 1.21: 0.88: 1.21. Interspaces; AME-AME 0.48, AME-ALE 0.39, PME-PME 1.07, PME-PLE 1.79, AME-PME 0.88, ALE-PLE 1.38. MOQ, aw: pw: l 2.50:2.79:2.62. Width of clypeus to AME 0.77.

*Labium.* L 2.7, W 2.9. Sternum: L 4.7, W 6.0.

*Legs.* (Table 1) Anterior leg indices; I 4.3, II 4.7.

*Spination.* Leg I; fe d101 p100 r111, pa p010 r010, ti d101 p101 r101 v222, mt p110 r110 v220, leg II; fe d101 p111 r111, pa p010 r010, ti d001 p101 r101 v222, mt p110 r110 v220, leg III; fe d101 p111 r101, pa p010 r010, ti p101 r101 v222, mt p110 r110 v220, leg IV; fe d101 p111 r001, pa p010, ti p101 r001 v222, mt p112 r112 v220, palp; fe 001 + 4 apically, pa p010 r010, ti d100 p111 r110, ta p111 r110.

*Epigynum.* Lateral rims somewhat parallel (Fig. 1D); fossa white. Vulva; spermathecal sacs long, arced anteriorly beyond insemination ducts then recurved (Fig. 1E), insemination ducts with 2½ coils (Fig. 1F).

Male (holotype *T. broomi*): CL 9.7, CW 8.8. AL 10.9, AW 8.0.

*Colour in alcohol.* As in Hogg (1902); differs from the female in the reddish chelicerae and maxillae and labium being orange-red.

*Eyes.* AME 0.78. AME:ALE:PME:PLE 1: 0.97: 0.77:1.03. Interspaces; AME-AME 0.18, AME-ALE 0.10, PME-PME 0.72, PME-PLE 1.03, AME-PME 0.54, ALE-PLE 0.77. MOQ, aw: pw: l 2:2.18:2.21. Width of clypeus to AME 0.46.

TABLE 1. Leg measurements of *T. barbata* (L. Koch), for F holotype *T. major* and male holotype *T. broomi* in parentheses.

| | Leg 1 | Leg 2 | Leg 3 | Leg 4 | Palp |
|---|---|---|---|---|---|
| Femur | 18.20 (14.85) | 20.50 (16.85) | 15.50 (12.10) | 16.40 (9.70) | 6.70 (4.50) |
| Patella | 8.40 (5.59) | 8.60 (6.10) | 6.50 (4.50) | 6.30 (2.30) | 3.20 (1.90) |
| Tibia | 17.90 (15.40) | 20.20 (17.21) | 13.20 (11.25) | 13.90 (9.20) | 4.70 (3.20) |
| Metatarsus | 18.70 (16.20) | 19.90 (17.20) | 12.80 (11.25) | 15.20 (8.70) | - - |
| Tarsus | 4.50 (3.81) | 4.50 (4.05) | 3.60(3.0 0) | 4.00 (2.95) | 6.80 (4.70) |
| Total | 67.70 (55.85) | 73.70 (61.40) | 51.60 (42.10) | 55.80 (32.85) | 21.40 (14.30) |

*Labium.* L 1.76, W 1.64. Sternum: L 5.21, W 4.40.

*Legs.* (Table 1) Anterior leg indices; I 5.8, II 6.3.

*Spination.* As female but; leg I; fe d001 p001, leg II; ti d101, palp; ti r010, ta 0.

*Palps.* Median apophysis small, apex sub-contiguous with conductor (Fig. 1I); embolus with 1¾ coils (Fig. 1G,H).

VARIATION. Carapace length of males; 7.76-13.16, mean 11.39 (n=6). Embolus with 1¾ - 2 coils. Carapace length of females; 13.20-18.25, mean 16.18 (n=34). Occasionally the fossa is narrow as in the syntype of *T. magnifica* (Fig 2C). Width of fossa divided by length of fossa of 34 females gave a range of 0.8- 1.27, the majority between 0.85 and 1.05 (Fig. 2).

DISTRIBUTION. Queensland, predominantly on the western side of the Great Dividing Range from Mt Isa eastwards to Allingham Creek (W of Townsville) southwards to NE NSW (Fig. 6).

REMARKS. Syntype material of *Isopeda barbata*, from Mackay, Qld and Sydney, NSW has not been found. The Mackay material was part of the Godeffroy Collection of which some was lodged in ZMH. ZMH holds only one specimen from Bowen and one from Rockhampton (neither examined) while the syntype whereabouts is unknown, but H. Dastych (pers. comm.) considers it improbable it was sold to any other museum. Further, part of that material from ZMH was lost during WW II. The syntype is not in other museums to which material was sold or

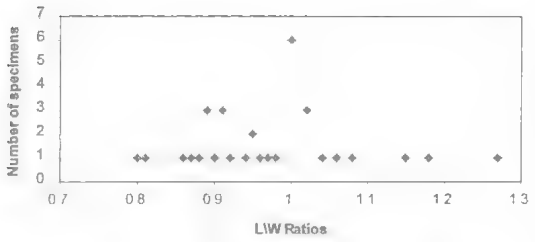



FIG. 2. *Typostola barbata* epigynal L/W ratios.

likely to have been deposited (BMNH, HNHM, MNHP, NHMW, NHRM, NM, SMNS, or ZMB), but BMNH has a male and a juvenile from Port Mackay and MNHP a male from Rockhampton (examined) both of which are from later collections. Material from Sydney was lodged in the Bradley Collection (MMUS) some of which is held by AM. This material has not been found in those collections nor in the collections of other Australian Museums. L. Koch (1875; pl. 56, fig. 3) figured the epigynum of *T. barbata* in which the posterior corners of the lateral rims are shown to almost converge. This is an unusual situation in the Deleninae and is considered to be an error. Measurements taken from the drawing give a value of 0.88, within the range given under Variation above. Koch has also illustrated the palp femora as proportionally longer than usual with the total length of the palp being greater than given in the text. This is considered a deliberate error to better illustrate the dense setae present retroventrally, said by Koch to be 'unten', but appearing as proventral in his illustration. As all material examined agrees otherwise with the original description, designation of a neotype is considered unnecessary. *T. barbata* differs from all other species in possessing plumose setae on the chelicerae, maxillae, and palpal trochanter, femora and tarsi.

**Typostola tari** sp. nov.
(Figs 3,6; Table 2)

ETYMOLOGY. For the type locality, Tari, PNG.

MATERIAL. HOLOTYPE: MVK-4104, M, Tari, 5°52'S 142°58'E, PNG, Nov-Dec 1977, A.J. Coventry.

DIAGNOSIS. Male. AME largest. Colour dark red-brown with brown-black stripes ventrally on the abdomen; sternum with dense adpressed yellow setae medially. Tibial apophysis short, broad. Median apophysis oval, large; embolus with 2 coils. Female unknown.

DESCRIPTION. Male (holotype): CL 13.48, CW 11.77. AL 13.75, AW 9.30.

*Colour in alcohol.* Carapace red-brown, caput darker, ocular area with yellow setae mainly around PME. Chelicerae dark red-brown, long yellow setae. Maxillae and labium black-brown, anterior margins reddish. Sternum red-brown, dense yellow recumbent setae except on margins, long upright brown setae. Coxae red-brown with brown suffusion. Legs red-brown, long grey and yellow-brown setae. Abdomen with dense yellow, brown and white setae; venter yellow with brown-black stripes (Fig. 3E), anterior of epigastric furrow black-brown but lung-books green.

*Eyes.* AME 1.01. AME:ALE:PME:PLE 1:0.97: 0.69: 0.81. Interspaces; AME-AME 0.30, AME-ALE 0.22, PME-PME 1.00, PME-PLE 1.15, AME-PME 0.73, ALE-PLE 0.74. MOQ, aw: pw: 1 2.30:2.39:2.38. Width of clypeus to AME 0.61.

*Labium.* L 1.32, W 1.46. Sternum: L 6.51, W 5.48.

*Legs.* (Table 2) Anterior leg indices; I 5.3, II 5.5.

*Spination.* As F *T. barbata* but leg I; fe p111, leg II-IV; pa p0, palp; ti r010, ta 0.

TABLE 2. Leg measurements of *T. tari* sp. nov., for holotype male.

| | Leg 1 | Leg 2 | Leg 3 | Leg 4 | Palp |
|---|---|---|---|---|---|
| Femur | 18.81 | 20.69 | 15.71 | 16.90 | 5.68 |
| Patella | 7.62 | 7.80 | 6.28 | 5.79 | 2.69 |
| Tibia | 19.80 | 20.69 | 14.56 | 15.12 | 3.51 |
| Metatarsus | 20.14 | 20.70 | 13.95 | 16.68 | - |
| Tarsus | 4.65 | 4.72 | 3.93 | 4.66 | 5.73 |
| Total | 71.02 | 74.60 | 54.43 | 59.15 | 17.61 |

*Palps.* Median apophysis oval (Fig. 3D), apex subcontiguous with conductor; embolus with 2 coils (Fig. 3A,B).

Female. Unknown.

DISTRIBUTION. *T. tari* is known only from the type locality, Tari, PNG (Fig. 6).

REMARKS. The male of *T. tari* is similar to *T. barbata*, but differs in being darker in colour, in the venter pattern, in lacking plumose setae and in having a short, broad tibial apophysis and larger median apophysis. The female is unknown.




FIG. 3. *Typostola tari* sp. nov. male holotype. A, B, left palp; A, ventral, B, retrolateral; C, chelicera, left, ventral; D, median apophysis; E, abdomen, venter. Scale bars; A, B = 0.5mm, C, E = 1mm, D, not to scale.

**Typostola heterochroma** sp. nov.
(Figs 4, 6; Table 3)

ETYMOLOGY. For the varied colour of this species, *hetero*, Greek = different and *chroma*, Greek = colour.

MATERIAL. HOLOTYPE: AMKS16546, F, Moonpah S.F., nr Dorrigo, 30°18'S 152°40'E, New South Wales, Mar 1986, M. Sawtell. ALLOTYPE: QMS35387, M, Cunninghams Gap (Main Range Natl Park), 28°03'S 152°24'E, Qld, 20.ii.1971, B. Baldwin.

DIAGNOSIS. Colour yellow-red. ALE largest; lateral eyes on low mound. Chelicera setose without beard; distal retromarginal tooth largest. Male palpal tibial apophysis relatively short, blunt; median apophysis elongate; embolus with 3½ coils apically. Female spermathecal sacs long, arced to anterior; insemination ducts with 4¼ lightly sclerotised coils.

DESCRIPTION. Female (holotype): CL 13.65, CW 12.98. AL 19.10, AW 14.65.

*Colour in alcohol*. Carapace red-brown, brown suffusion, sparse brown setae, yellow-white adpressed setae in ocular area. Chelicerae dark red-brown. Maxillae and labium black, reddish towards anterior margins. Sternum orange-red,

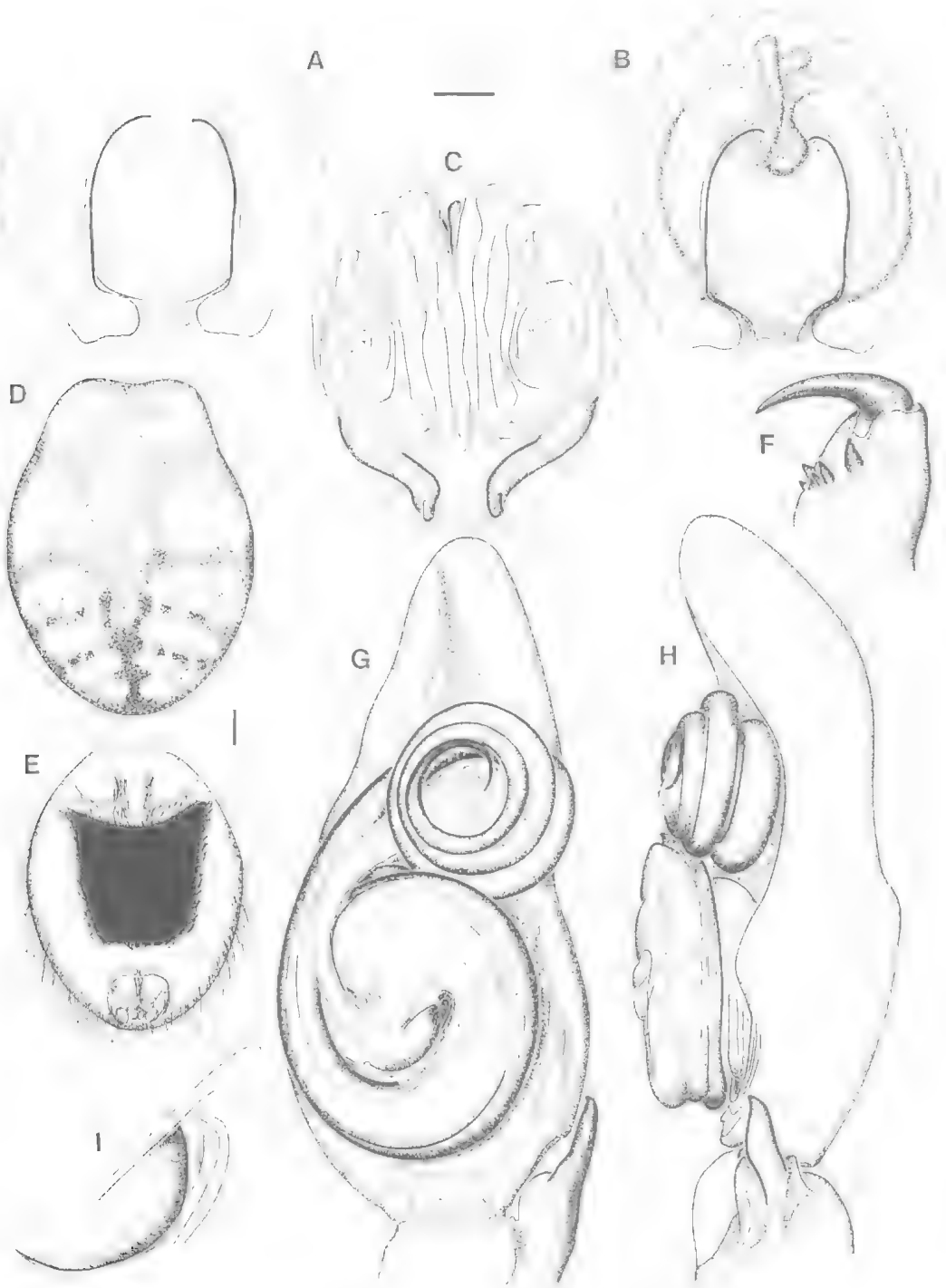



FIG. 4. *T. heterochroma* sp. nov. A-D, female holotype. A, epigynum; B, epigynum cleared, ventral; C, vulva, dorsal; D, abdomen, dorsal: E-I, male allotype. E, abdomen, ventral; F, chelicera, left, ventral; G, H, left palp, G, ventral, H, retrolateral; I, median apophysis. Scale bars; A-C, G, H = 0.5mm, D-F = 1mm, I, not to scale.

TABLE 3. Leg measurements of *T. heterochroma* sp. nov., for holotype female and allotype male in parenthesis.

| | Leg 1 | Leg 2 | Leg 3 | Leg 4 | Palp |
|---|---|---|---|---|---|
| Femur | 14.68 (16.26) | 16.67 (18.47) | 12.41 (13.31) | 12.73 (14.34) | 5.52 (5.19) |
| Patella | 7.37 (7.14) | 7.49 (7.59) | 5.56 (5.48) | 5.07 (4.97) | 2.68 (2.12) |
| Tibia | 13.49 (16.29) | 15.65 (19.66) | 9.97 (12.64) | 10.80 (12.53) | 3.51 (2.92) |
| Metatarsus | 13.99 (16.68) | 15.48 (18.31) | 9.24 (10.75) | 11.37 (13.12) | - - |
| Tarsus | 3.63 (4.07) | 3.70 (4.16) | 2.05 (3.20) | 3.20 (3.50) | 5.65 (4.41) |
| Total | 63.16 (60.44) | 58.99 (68.19) | 39.23 (35.38) | 43.17 (48.46) | 17.36 (14.64) |

long yellow-white setae. Legs red-brown, yellow--brown setae. Abdomen cream-yellow, indistinct folium and posterior chevrons (Fig. 4D), long dense yellow-brown setae, laterals cream-yellow; venter with large brown badge covered with yellow--brown setae.

*Eyes*. AME 0.77. AME:ALE:PME:PLE 1: 1.13: 0.73: 1.03. Interspaces; AME-AME 0.53, AME-ALE 0.55, PME-PME 1.61, PME-PLE 1.84, AME-PME 0.97, ALE-PLE 1.12. MOQ, aw: pw: 1 2.53:3.06:2.73. Width of clypeus to AME 0.73.

*Labium*. L 2.32, W 2.88. Sternum: L 6.48, W 5.77.

*Legs*. (Table 3) Anterior leg indices; I 3.9, II 4.3.

*Spination*. As in male *T. barbata* but leg I; fe p110.

*Epigynum*. Lateral rims somewhat parallel (Fig. 4A); anterior of fossa recessed. Vulva with spermathecal sacs extending just anterior of fertilisation ducts (Fig. 4B), insemination ducts lightly sclerotised and with 4¼ coils (Fig. 4C).

Male (allotype): CL 12.47, CW 11.18, AL 12.70, AW 8.60.

*Colour in alcohol*. As female except as follows; carapace yellowish on laterals, caput darker red-brown, fovea reddish. Leg femora, patellae and tibiae red dorsally, yellow ventrally; metatarsi and tarsi dark orange-brown. Venter abdomen (Fig. 4E).

*Eyes*. AME 0.75. AME:ALE:PME:PLE 1: 1.12: 0.79: 1.01. Interspaces; AME-AME 0.51, AME-ALE 0.41, PME-PME 1.35, PME-PLE 1.49, AME-PME 0.89, ALE-PLE 0.97. MOQ, aw: pw: 1 2.51:2.93:2.69. Width of clypeus to AME 0.77.

*Labium*. L 2.16, W 2.49. Sternum: L 6.13, W 5.31.

*Legs*. (Table 3) Anterior leg indices; I 4.9, II 5.5.

*Spination*. As female but leg II; ti d001; palp; pa p0, tarsus 0.

*Palps*. Median apophysis elongate (Fig. 4I), apex contiguous with conductor; embolus with 3½ coils (Fig. 4G,H).

DISTRIBUTION. Known only from near Dorrigo on the E side of the Great Dividing Range in northern NSW and Cunninghams Gap from central Great Dividing Range in SE Qld (Fig. 6).

REMARKS. *T. heterochroma* differs from all other species in having the distal retromarginal tooth largest. It further differs from *T. barbata* in lacking plumose setae and in having 3½ male embolic coils and 4½ female insemination duct coils. It is most similar to *T. pilbara* in female insemination duct coils but differs in the venter pattern and fossa shape.

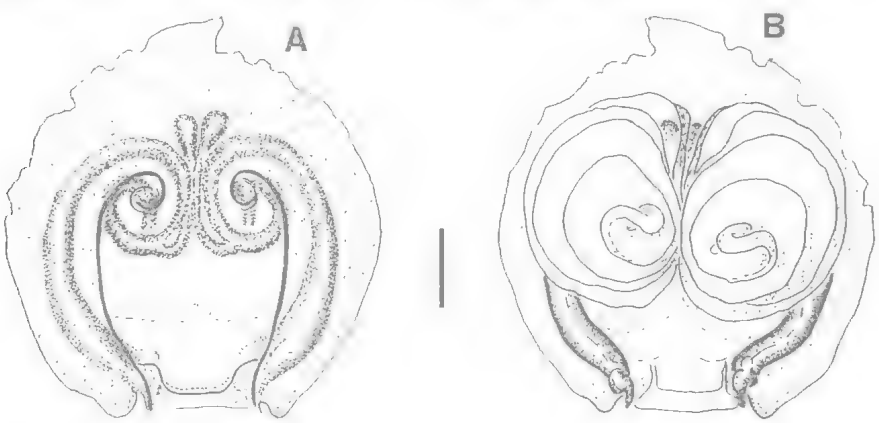



FIG. 5. *T. pilbara* sp. nov. F holotype. A, epigynum ventral, cleared; B, vulva, dorsal Scale bar = 0.5mm.

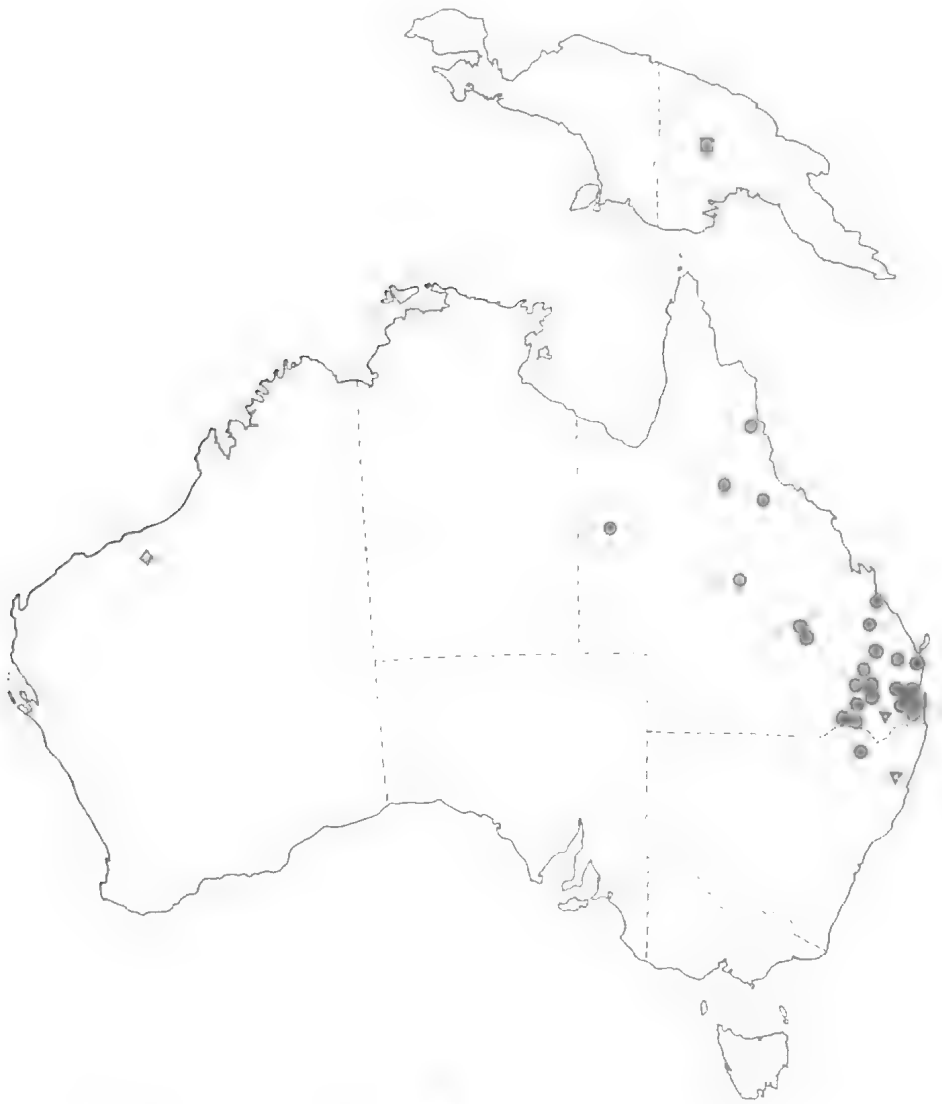


FIG. 6. Distribution of *T.* spp. *T. barbata* (L. Koch) ●; *T. heterochroma*, sp. nov. ▼; *T. pilbara*, sp. nov. ◆; *T. tari*, sp. nov. ■.

**Typostola pilbara** sp. nov.
(Figs 5,6; Table 4)

ETYMOLOGY. In apposition to the Pilbara region in which Marble Bar lies.

MATERIAL. HOLOTYPE: WAM88/870, F, Coppin Gap, Marble Bar, 20°53'S 120°07'E, Western Australia, 13.i.1970, M. deGraaf. PARATYPE: WAM14/850, F, Marble Bar, 21°10'S 119°44'E, Western Australia, 7.vii.1914, Dr Thorp.

DIAGNOSIS. Female. ALE largest. Colour yellow-brown. Female epigynum with insemination duct openings in fossa anteriorly, insemination ducts with 4½ coils, vulva with anteriorly curved spermathecal sacs extending to anterior of insemination ducts. Male unknown.

DESCRIPTION. Female (holotype): CL 12.26, CW 10.39. AL 11.95, AW 8.30.

*Colour in alcohol.* Carapace yellow-brown, red-brown suffusion, fovea reddish, ocular area red-brown. Upright brown setae, adpressed long fine yellow-white setae. Chelicerae red-brown. Maxillae and labium orange-brown. Sternum yellow-orange, dense white setae on margins.

TABLE 4. Leg measurements of *T. pilbara* sp. nov., holotype female.

| | Leg 1 | Leg 2 | Leg 3 | Leg 4 | Palp |
|---|---|---|---|---|---|
| Femur | 15.93 | 17.29 | 14.20 | 16.12 | 4.65 |
| Patella | 6.71 | 6.88 | 5.58 | 5.47 | 2.48 |
| Tibia | 15.48 | 16.33 | 12.19 | 13.69 | 3.70 |
| Metatarsus | 16.82 | 18.16 | 12.04 | 15.69 | - |
| Tarsus | 3.74 | 3.80 | 3.17 | 3.31 | 5.30 |
| Total | 58.68 | 62.46 | 47.18 | 54.28 | 16.13 |

Coxae I with dense yellow setae prolaterally. Legs yellow-brown, darker around bases of heavier setae. Abdomen yellow-brown, dense yellow, white and brown setae; venter yellow, yellowish setae.

*Eyes*. AME 0.66. AME:ALE:PME:PLE 1: 1.18:0.85:0.97. Interspaces; AME-AME 0.53, AME-ALE 0.15, PME-PME 1.15, PME-PLE 1.30, AME-PME 1.12, ALE-PLE 0.89. MOQ, aw: pw: l 2.53:2.85:3.06. Width of clypeus to AME 0.57.

*Labium*. L 1.94, W 2.26. Sternum: L 5.58, W 4.93.

*Legs*. (Table 4) Anterior leg indices; I 4.8, II 5.1.

*Spination*. As in female *T. barbata* but Leg I; fe p 111, leg II, ti d101, leg III; fe r111 ti d101, leg IV; ti d101.

*Epigynum*. (Fig. 5A,B) Insemination ducts with 4½ coils.

Male. Unknown.

VARIATION. Paratype female with carapace length of 10.58.

DISTRIBUTION. *T. pilbara* is known only from the Marble Bar area in WA (Fig. 6).

REMARKS. *T. pilbara* is similar to *T. heterochroma* but differs in the comparatively uniform colour pattern and in possessing small insemination duct openings in the anterior of the fossa.

ACKNOWLEDGEMENTS

I thank the following people who provided material for study: M. Gray and C. Horseman (AM), P. Hillyard (BMNH), M. Harvey and J. Waldock (WAM), R. Raven and P. Lawless (QM) and C. Rollard (MNHP). P. Jäger provided information concerning heteropodid types held in NM. H. Dastych (ZMH), J. Gruber (NHMW), T. Kronestedt (NHRM), M. Grasshoff (SMF), S. Mahunka (HNHM), V. Matthews (MMUS) and S. Nawal (ZMB) are also thanked for responding to my enquiries.

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# REVISION OF *AULOSPONGUS* AND OTHER RASPAILIIDAE WITH RHABDOSTYLES (PORIFERA: DEMOSPONGIAE: POECILOSCLERIDA)

JOHN N.A. HOOPER, HELMUT LEHNERT AND SVEN ZEA

Hooper, J.N.A., Lehnert, H. & Zea, S. 1999 06 30: Revison of *Aulospongus* and other Raspailiidae with rhabdostyles (Porifera: Demospongiae). *Memoirs of the Queensland Museum* **43**(2): 649-707. Brisbane. ISSN 0079-8835.

*Aulospongus* is revised to contain 10 species (*cerebella* Dickinson, *flabellum* Pultizer-Finali, *gardineri* (Dendy), *involutum* (Kirkpatrick), *monticularis* (Ridley & Dendy), *novaecaledoniensis* sp. nov., *samariensis* sp. nov., *spinosum* (Topsent), *tubulatus* (Bowerbank) and *villosa* (Thiele)). Other species previously included in *Aulospongus* are referred to *Raspailia* (*Raspaxilla*), most being new combinations. *Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*) are also reviewed and some re-illustrated, containing 17 and 1 species, respectively. *Aulospongus* is contrasted with these genera, differing in having two homologous size categories of rhabdostyles, apparently of common derivation, coring and echinating fibres; plumose skeletal structure persisting throughout choanosomal and peripheral skeletons composed of ascending compressed fibre-bundles with few or no reticulate elements; lacking any differentiation between axial and extra-axial skeletons. Phylogenetic analysis delineates 2 groups of *Aulospongus* species based primarily on skeletal structure: one group exclusively plumose, the other with rudimentary plumo-reticulate skeletons, with the non-rhabdose raspailiid outgroup predominantly plumo-reticulate or reticulate, with loss of ectosomal specialisation being highly homoplasic and unstable throughout the classification of Raspailiidae. Biogeographic comparisons among rhabdose raspailiids (*Aulospongus* versus *Raspaxilla* and *Hemectyon*) show essential differences in distributions (pan-equatorial versus Pacific rim, respectively). ❐ *Porifera, Demospongiae, Raspailiidae, Aulospongus, Raspaxilla, Hemectyon, new species, new records, new combinations, taxonomic revision, rhabdostyles.*

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Rhabdostyles (structural stylote megascleres with a prominent bend or rhabd at the basal extremity), are found amongst several groups of demosponges. They have been recorded from the order Poecilosclerida, families Raspailiidae (*Aulospongus* Norman, *Raspaxilla* Topsent, *Echinaxia* Hallmann, *Axinectya* Hallmann, *Hemectyon* Topsent), Rhabderemiidae (*Rhabderemia* Topsent), and Desmacellidae (*Biemna* Gray), and order Halichondrida, families Desmoxyidae (*Halicnemia* Bowerbank, *Higginsia* Higgin), and Axinellidae (*Rhabdoploca* Topsent, *Hymerhabdia* Topsent, *Lithobubaris* Vacelet, *Monocrepidium* Topsent, *Perissinella* Topsent), with the implication that they have been derived independently within each group (homoplasic developments).

Amongst Raspailiidae there may be two forms of rhabdostyles. Smaller echinating (usually acanthose) rhabdostyles occur in the three rhabdose genera, and are probably homologous to typical echinating acanthostyles found throughout Raspailiidae. In *Raspaxilla* (including the synonyms *Echinaxia* Hallmann, *Axinectya* Hallmann) and *Hemectyon* Topsent, as in most raspailiids, fibres are cored by non-rhabdose, smooth styles of distinctly different geometry and origin from the rhabdose echinating spicules. In *Aulospongus* larger, smooth or partially spined choanosomal principal rhabdostyles bear a strikingly resemblance to the smaller rhabdostyles, from which they are probably derived. Nevertheless, despite these apparently straightforward generic differences there are several species currently assigned to *Aulospongus* that do not easily rest there, mostly because they possess characters intermediate to both groups.

The present work revises *Aulospongus*, as a consequence of discovering several characters in the type species (*A. tubulatus*); redescribes and illustrates all known species; describes a new

species from the Caribbean fauna (a new locality record for the genus), and New Caledonia; and reviews and compares all known species of raspailiids with rhabdostyles (*Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*).

*Aulospongus* presently contains 15 species (Hooper, 1991; Pulitzer-Finali, 1993; Desqueyroux-Faundez & van Soest, 1997), including the two new species described in this present work, whereas five of these species are referred here to *Raspailia* (*Raspaxilla*) based on major differences between the two genera in their skeletal structure and geometry of structural megascleres.

*Aulospongus*, as revised here, contains 10 species and has a disjunct geographic distribution, from the N Atlantic (São Vicente and Cape Verde Islands), SW Indian Ocean (Natal), W and central Indian Ocean (Zanzibar, Kenya, Gulf of Aden, Arabian Gulf, S Arabian coast, Amirante, India, Sri Lanka), NW Pacific (Japan) and SW Pacific Ocean (New Caledonia), E Pacific (Gulf of California), and Caribbean (Colombia and Jamaica). *Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*) now contain 17 and 1 species, respectively, with wide but very different patterns of distribution than *Aulospongus*.

Australasian and New Caledonian raspailiid faunas (Hooper, 1991; Hooper & Lévi, 1993) are well known compared to most regional faunas, containing 56 and 7 species, respectively. To date there has not been any synthesis of the published Caribbean raspailiid fauna (including the Gulf of Mexico and West Indies),with species records scattered throughout many isolated publications (e.g. see Wiedenmayer, 1977; Zea, 1987). It is therefore appropriate to list the published fauna here, containing 20 raspailiid species for the entire region. These include: Genus *Ceratopsion* Strand (*C. crustosum* Alvarez & van Soest, 1993: 629). Genus *Cyamon* Gray (*C. vickersi* (Bowerbank, 1864: 234) (Dendy, 1922: 109; Arndt, 1927: 149; Pulitzer-Finali, 1986: 199; van Soest & Stentoft, 1988: 115; Hooper, 1991: 1304)). Genus *Ectyoplasia* Topsent (*E. ferox* (Duchaissaing & Michelotti, 1864: 81) (Wiedenmayer, 1977: 158; Pulitzer-Finali, 1986: 105, 199; Zea, 1987: 202; van Soest et al., 1983: 198, 204; Hooper, 1991: 1273)). Genus *Endectyon* Topsent (*E. tenax* (Schmidt, 1870: 62) (Topsent, 1920: 23; Wells et al., 1960: 218; Pulitzer-Finali, 1986: 199; Hooper, 1991: 1284); *E.* (*Hemectyon*) *hamatum* (Schmidt, 1870: 62) (Topsent, 1920: 26; Pulitzer-Finali, 1986: 199; Hooper, 1991: 1285)). Genus *Echinodictyum* Ridley (*E. lugubre* (Duchaissaing & Michelotti, 1864: 89) (de Laubenfels, 1936: 63; Wiedenmayer, 1977: 254; Pulitzer-Finali, 1986: 106, 199; Hooper, 1991: 1349); *E. pennatum* (Duchaissaing & Michelotti, 1864: 88) (de Laubenfels, 1936: 63; Wiedenmayer, 1977: 254; Pulitzer-Finali, 1986: 199; Hooper, 1991: 1349)). Genus *Eurypon* Gray (*E. clavatella* Little, 1963: 49 (Pulitzer-Finali, 1986: 199); *E.* cf. *clavatum* (Bowerbank, 1866: 143) (sensu Topsent, 1889: 29; Wells et al., 1960: 217; Desqueyroux-Faundez, 1981: 737; Pulitzer-Finali, 1986: 199; Hooper, 1991: 1314); *E. coronula* (Bowerbank, 1874: 246) (Topsent, 1936: 66; Pulitzer-Finali, 1986: 199); *E. laughlini* Diaz et al., 1987: 33; *E. topsenti* (Burton, 1954: 235); *E. toureti* (Topsent, 1894: 30); *E. viride* (Topsent, 1889: 43) (de Laubenfels, 1950: 81; Wiedenmayer, 1977: 160; Pulitzer-Finali, 1986: 199; Hooper, 1991: 1314)). Genus *Plocamione* Topsent (*P. clopetaria* (Schmidt, 1870: 63) (Burton, 1935: 402; Pulitzer-Finali, 1986: 203; van Soest & Stentoft, 1988: 115; Hooper, 1991: 1319). Genus *Raspailia* Nardo (*R. acanthifera* (George & Wilson, 1919: 159); *R. pearsi* (Wells et al., 1960: 218); *R. cf. tenuis* Ridley & Dendy, 1886 (van Soest & Stentoft, 1988: 113). Genus *Thrinacophora* Ridley (*T. spinosa* Wilson, 1902: 400 (Pulitzer-Finali, 1986: 199; Hooper, 1991: 1340); *T. funiformis* Ridley & Dendy, 1886: 484 (1887: 195; Zea, 1987: 198; Hooper, 1991: 1339)).

## MATERIALS AND METHODS

Terminology for Raspailiidae follows Hooper (1991). Preparation techniques for light microscopy follows Hooper (1996). Spicule measurements are based on 25 random samples of each spicule category for each species, indicated as range of lengths and widths, or range (and mean) for the new taxa. Spicule and section illustrations were produced using digital light microscopy. Phylogenetic analyses were performed using Paup 3.1.1 (Swofford, 1993), and character changes further explored with MacClade (Maddison & Maddison, 1992). Statistical support for phylogenetic tree branching was undertaken using Bootstrap index (under Paup) and Autodecay (Version 3.0; Eriksson & Wikstrom, 1997). The latter index measures Bremer (Branch) support for the nodes. Bremer (1994) defined branch support as the extra total tree length needed for the specified

branch to be lost in the strict consensus of near-most parsimonious tree. The Autodecay program examines a consensus of all trees of a certain length, increasing by 1 from the most parsimonious tree (MPT) length, and saves the consensus trees until all the nodes in the MPT have disappeared. It then determines the Branch Support by counting the increase in the length before that particular node disappeared. Decay values of <0 indicate that MPT has been constrained and that shorter, unconstrained trees may exist, or that an error has been made with the MPT length. Decay value of 0 indicates there are other MPTs which do not have this branch; and values >1 indicate that all MPTs have this node, with potential level of statistical support for nodes increasing on a scale of 1-10.

Abbreviations: AHF, Alan Hancock Foundation (University of Southern California, Los Angeles); AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; ICN-MHN, Istituto de Ciencias Naturales – Museo de Historia Natural (Porifera collection) – Universidad Nacional de Colombia, AA 74-95, Santafé de Bogotá DC, Colombia; INV, Instituto de Investigaciones Marinas y Costeras 'José Benito Vives de Andreis'; INVEMAR, Porifera collection, AA 10-16, Santa Marta, Colombia; MOM, Musée Oceanographie Monaco; MNHN, Muséum National d'Histoire Naturelle, Paris; Munsell: Munsell color charts (Munsell, 1977); MSNG, Museum of Natural History of Genoa; MZUS, Museé Zoologique de Strasbourg, France; NCG, Naturalist's Color Guide (see Smithe, 1975); MONZ, National Museum of New Zealand (Dominion Museum), Wellington; NTM, Northern Territory Museum of Arts and Sciences, Darwin; ORSTOM, Institut Français de Recherche Scientifique pour le Developpement en Cooperation, Centre de Noumea; QM, Queensland Museum, Brisbane; USC, University of Southern California, Los Angeles; USNM, National Museum of Natural History, Smithsonian Institution, Washington; ZMA, Zoological Museum, University of Amsterdam; ZMB, Zoologisches Museum für Naturkunde an der Humboldt-Universität zu Berlin.

## ACKNOWLEDGEMENTS

We thank Rob van Soest and Belinda Alvarez de Glasby for their comments which greatly improved this manuscript. We also thank M.G. (Jojo) Bargibant (ORSTOM Centre de Noumea) for kindly providing the photograph of *Raspailia (Raspaxilla) clathrioides*; Ms Kylie Dwine (QM) for digital spicule imaging; Prof. Jerry Bakus (USC) for searching for AHF type material; Dr Klaus Ruetzler and Ms Kathleen Smith (USNM), Ms Clare Valentine (BMNH), Prof. Claude Lévi (MNHN), and Dr Deiter Kühlman (ZMB) for the loan of type material. Sven Zea's work is Contribution No. 614 of the Instituto de Investigaciones Marinas y Costeras 'José Benito Vives de Andreis' - INVEMAR, and No. 148 of the Marine Biology Graduate Program of the Universidad Nacional de Colombia, Faculty of Sciences.

## SYSTEMATICS

### Family **Raspailiidae** Hentschel, 1923

KEY TO GENERA WITH RHABDOSTYLES. Those genera with echinating acanthostyles with basal rhabds.

1. Both smaller echinating (acanthose) styles and larger choanosomal (smooth or acanthose) principal styles have basal rhabds with more-or-less similar geometry; both categories of rhabdostyles distributed throughout the skeleton, the latter predominantly confined within fibres; axial skeleton slightly more compressed but otherwise virtually undifferentiated from the extra-axial skeleton, both regions dominated by ascending plumose fibre-bundles . . . . . *Aulospongus*

   Choanosomal principal styles geometrically different from echinating rhabdostyles/acanthostyles; choanosomal principal styles entirely smooth, without basal rhabd, often with anisoxeote/strongylote modifications; axial and extra-axial skeletons well differentiated . . . . . 2

2. Echinating rhabdostyles predominant in (although not strictly localised to) peripheral skeleton; axial skeleton compressed and more-or-less reticulate; extra-axial skeleton plumoreticulate cored by choanosomal principal styles and longer subectosomal extra-axial styles, with transverse fibres/tracts interconnecting ascending plumose tracts/fibres all the way to the surface, or reduced to a radial skeleton of single subectosomal extra-axial spicules . . . . . *Raspailia (Raspaxilla)*

   Echinating acanthostyles with clavulate spines on apex, bases smooth and sometimes with slight basal rhabd; echinating spicules localised at junction of axial and extra-axial skeletons, outside the axis (in compressed forms with radial extra-axial skeleton) or echinating plumose extra-axial fibres, and often producing spicule brushes at the surface . . . . *Endectyon (Hemectyon)*

### **Aulospongus** Norman, 1878

*Aulospongus* Norman, 1878: 267; Dendy, 1889: 89; Dendy, 1922: 61; Burton, 1938: 38; Hooper, 1991: 1307; Hooper & Lévi, 1993: 1294 (not *Aulospongus*; de Laubenfels, 1936: 100). Type species *Haliphysema tubulatus* Bowerbank, 1873: 29 (by original designation).

*Heterectya* Hallmann, 1917: 393. Type species: *Raspailia (?) villosa* Thiele, 1898: 60 (by original designation).
*Rhaphidectyon* Topsent, 1927: 15. Type species: *Rhaphidectyon spinosum* Topsent, 1927: 15 (by original designation and monotypy; schizotypes MNHN LBIM DT 1139, BMNH 1930.7.1.39).
*Aulospongiella* Burton, 1956: 141. Type species *Axinella monticularis* Ridley & Dendy, 1886: 481 (by original designation and monotypy).
*Hemectyonilla* Burton, 1959: 254. Type species: *Stylostichon involutum* Kirkpatrick, 1903: 250 (by original designation and monotypy).

DEFINITION. Raspailiidae with at least two size classes of rhabdostyles of similar geometry, the larger (smooth or partially spined) core spongin fibres, and the smaller (partially spined) echinate fibres although neither are localised to any region of the skeleton; choanosomal skeletal structure is predominantly plumose, with spicules and fibres amalgamated into bulbous tracts ('fibre-bundles'), more-or-less complicated in the axial skeleton, becoming increasingly plumose as they ascend to the periphery, eventually producing a shaggy, compartmentalised or conulose surface; axial and extra-axial skeletons undifferentiated apart from greater amalgamation of fibre-bundles in the axis.

DIAGNOSIS (emended). Growth forms tubular, cup-shaped, lobate, lamellate or erect cylindrical-digitate; individual lobes or branches are composed of large fibre-bundles amalgamated at the core or base of the sponge, diverging and becoming increasingly plumose towards the periphery, eventually producing a compartmentalised surface of discrete lobes or shaggy surface processes. Ectosomal skeleton ranges from: well developed, 'specialised raspailiid' (consisting of long subectosomal extra-axial styles protruding through the surface, surrounded by sparse brushes of ectosomal auxiliary spicules); vestigial (with wispy raphidiform or sinuous ectosomal auxiliary spicules scattered sparsely and indiscriminately over the surface); or absent completely (with only choanosomal principal spicules protruding through the surface, forming discrete surface bundles). Long subectosomal extra-axial spicules produce a hispid surface in some species. Choanosomal skeletal structure predominantly plumose (with very few reticulate connecting fibres, and these mainly towards the axis), with virtually no differentiation between axial and peripheral skeletons. Ascending fibres nearly fully cored by larger choanosomal principal rhabdostyles, forming dense plumose bundles particularly on fibre nodes, and echinated by smaller rhabdostyles, together producing bulbous spiculo-spongin tracts (termed here 'fibre-bundles'); smaller echinating rhabdostyles more-or-less evenly dispersed throughout the skeleton; interconnecting fibres, if present, are aspicular or paucispicular, and generally confined to the axial region. Megascleres consist of larger choanosomal principal rhabdostyles usually with a relatively slight basal rhabd, entirely smooth or with recurved spines only on apical part of spicules. Smaller echinating rhabdostyles in one or two categories have more pronounced basal rhabd, often prominently subtylote, entirely smooth or with spines only the apex of spicules, or covering most of the spicule except for the base, or rarely completely spined. Subectosomal extra-axial styles or anisoxeas, if present are long and protrude through the surface. Ectosomal auxiliary styles or anisoxeas, if present, are wispy, sinuous or raphidiform, often vestigial. Raphide microscleres are present in only one species.

**Aulospongus tubulatus** (Bowerbank, 1873)
(Figs 1-2, Table 1)

*Haliphysema tubulatus* Bowerbank, 1873: 29, pl. 7.
*Aulospongus tubulatus*; Norman, 1878: 267; Dendy, 1905: 176; Dendy, 1922: 61; Burton & Rao, 1932: 347; Burton, 1938: 32, pl. 3, fig. 24; Burton, 1959: 253; Thomas, 1985: 269, pl. 3, fig. 10; Hooper, 1991: 1307, fig. 66g-k.
*Axinella tubulata*; Dendy, 1889: 89, pl. 5, fig. 11.

MATERIAL. HOLOTYPE. BMNH1873.7.21.9: Ceylon (Sri Lanka), coll. E.W.H. Holdsworth. OTHER MATERIAL. BMNH1931.11.28.18 (fragment MNHNLBIMDCL51): Off Megapatam, Amirante, coll. 'Investigator', 16.vi.1930, 18-22m.

DISTRIBUTION. Amirante, Gulf of Aden, South Arabian Coast, SE coast India and Sri Lanka, W Indian Ocean.

DESCRIPTION. Growth form subspherical, massive, tubular, composed of amalgamated fibre-bundles that extend to the surface and produce a compartmentalised surface of discrete conules. Colour red or pinkish-red alive. Ectosome with vestigial 'raspailiid skeleton' composed of sinuous or raphidiform ectosomal auxiliary styles scattered sparsely and indiscriminantly over the surface, and with plumose bundles of both larger and smaller rhabdostyles protruding through the surface mainly at the ends of conules. No subectosomal extra-axial spicules. Adjacent surface conules interconnected by aspicular (membranous) collagen. Choanosomal skeleton exclusively

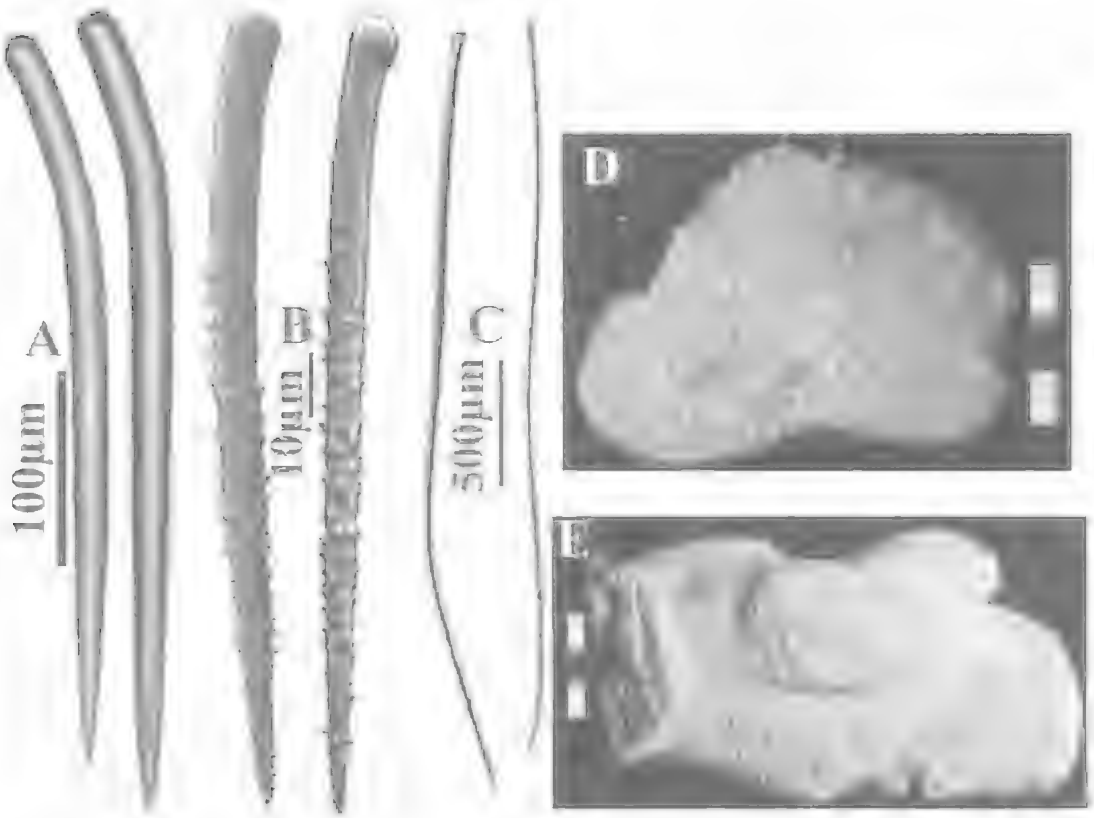



FIG. 1. *Aulospongus tubulatus*. A, Choanosomal principal rhabdostyles. B, Echinating rhabdostyles. C, Ectosomal auxiliary styles. D, Holotype (scale 3cm). E, 'Investigator' specimen (scale 3cm).

plumose with fibre-bundles fused relatively closely towards the base of the sponge and axis of the skeleton, becoming increasingly plumose towards the periphery, and eventually completely discrete/compartmentalised at the surface. Fibre-bundles composed of rhabdostyles, both coring and echinating fibres, forming ascending multispicular columns, branching or unbranched towards their apex, bonded together with light granular collagen. Larger smooth choanosomal principal rhabdostyles extend out from fibres in plumose bundles, particularly near periphery of skeleton. Smaller spined rhabdostyles heavily echinate fibres and fibre nodes. Megascleres consist of larger coring choanosomal principal rhabdostyles with slightly subtylote or rounded bases, slight basal rhabd, fusiform points, completely smooth (304-462×16-24µm). Smaller echinating rhabdostyles with entirely smooth, slightly rhabdose, slightly swollen bases, and small spines covering apical half of spicule (109-126×5-10µm). Long, thin, curved, sinuous or rhaphidiform ectosomal auxiliary styles (212-250×2-3µm). Subectosomal extra-axial spicules absent. Microscleres absent.

REMARKS. Re-examination of the holotype from Sri Lanka and Dendy's (1922) specimen from Amirante found the remnants of a specialised raspailiid ectosomal skeleton present in both, a character overlooked by previous authors, necessitating emendation to the generic diagnosis from that provided by Hooper (1991) and Hooper & Lévi (1993). This omission is not surprising given that the ectosomal skeleton in the type species is sparse and vestigial (consisting of wispy raphidiform anisoxeas scattered more-or-less indiscriminantly within the surface skeleton). Similarly, a more careful re-examination of *Stylostichon involutum* (the holotype of *Hemectyonilla*), also discovered these ectosomal auxiliary spicules to be present (consisting of a few wispy raphidiform oxeote spicules perpendicular to the surface). This confirms the synonymy between *Aulospongus* and *Hemectyonilla*, proposed tenuously by Hooper




FIG. 2. *Aulospongus tubulatus*. A, Choanosomal skeleton. B, Ectosomal skeleton.

(1991), and also provides more firm evidence in support of the inclusion of *Aulospongus* in Raspailiidae, previously considered to be atypical of the family.

A further consequence of these new findings is that *A. tubulatus* is no longer completely 'typical' of the genus, as defined by Norman (1878) and subsequently understood by other authors. Prior to this study the generic concept centred on the possession of a tubular growth form, only two categories of rhabdose megascleres (the larger coring and the smaller echinating fibres), exclusively plumose fibre-bundles, and lacking ectosomal specialisation and other spicules completely. However, *A. tubulatus* was found to have aspicular fibre connections between ascending plumose fibre-bundles, and ectosomal auxiliary spicules (albiet forming a vestigial ectosomal specialisation), necessitating re-evaluation of the genus and its relationships to *Raspaxilla* in particular. This is discussed futher below.

In having vestigial, scattered wispy ectosomal auxiliary spicules which do not necessarily form surface brushes *A. tubulatus* is similar to *A. involutum*, although the latter species also has larger subectosomal extra-axial styles erect on the surface. In having plumose fibre-bundles with few aspicular interconnecting tracts this species is also similar to *A. gardineri* and *A. novaecaledoniensis* sp.nov, although the two groups differ substantially in their spicule geometries. Other comparisons are given in Table 1.

**Aulospongus cerebella** (Dickinson, 1945)
(Fig. 3, Table 1)

*Heterectya cerebella* Dickinson, 1945: 22, pl. 34, figs 67-68.

*Aulospongus cerebella*; Desqueyroux-Faundez & van Soest, 1997: 442.

MATERIAL. HOLOTYPE. AHF no.11 (not seen): Isla Partida, Gulf of California, coll. 'Velero III', 9.iii.1936, 90m depth, sand substrate.

DISTRIBUTION. Known only from the Gulf of California.

DESCRIPTION. Growth form thickly lamellate or massively encrusting. Surface convoluted, meandering over substrate, highly conulose, with conules composed of irregularly fused, erect, fibre-bundles. Colour 'drab' in ethanol. 'Raspailiid ectosomal skeleton' absent although choanosomal principal styles protrude through surface forming conules. Choanosomal skeletal structure plumose, consisting of ascending fibre-bundles eventually forming surface conules, without any reticulate interconnecting tracts. Megascleres include larger, entirely smooth choanosomal principal rhabdostyles coring fibres, with only slight basal rhabd (600×35µm). Rhabdostyles echinating fibres, with smooth rhabdose bases, smooth shafts, and moderately small, granular spines only on the extreme points of spicules (400×30µm). Ectosomal auxiliary and subectosomal extra-axial spicules apparently absent. Microscleres absent (Dickinson, 1945).

TABLE 1. Summary of morphological comparisons between species of *Aulospongus* and type species (indicated by *) of *Raspaxilla* and *Hemectyon*.

| Species | Surface features & skeletal fibre-bundles | Skeletal reticulation & axial vs. extra-axial skeleton | Choanosomal principal spicules (spicule size) | Echinating spicules (spicule size) | Specialised ectosomal auxiliary skeleton (spicule size) | Subectosomal extra-axial spicules (spicule size) | Raphides (spicule size) |
|---|---|---|---|---|---|---|---|
| **A. tubulatus* | Discrete surface conules, not hispid; fibre-bundles present | Very slight retic-ulation with few aspicular fibre connections; undifferentiated axial/extra- axial skeleton | Slightly rhabdose and subtylote, entirely smooth (304-462× 16-24μm) | Slightly rhabdose and subtylote, spines on apical third, spines small and slightly re-curved (109-126×5-10μm) | Vestigial, sinuous rhaphidiform styles scattered on surface (212-250×2-3μm) | Absent | Absent |
| *A. cerebella* | Surface convo-luted, conulose, not hispid; fibre-bundles present | No reticulation; undifferenti-ated axial/ exra- axial skeletons | Slightly rhabdose, entirely smooth (600×35μm) | Strongly rhabdose, spines only on points, spines gran-ular (400×30μm) | Absent, only choanosomal principal styles protrude through surface | Absent | Absent |
| *A. flabellum* | Surface with longitudinal ridges and dis-tinct osculi-ferous and porous faces; fibre-bundles ? | Unknown | Slightly rhabdose, entirely smooth (340-570× 16-34μm) | Faintly rhabdose, spines mostly on points, bases and central portion, or more-or-less evenly spined (120-370×11-19μm) | Absent, with only larger choan-osomal principal rhabdostyles protruding through surface | Absent | Absent |
| *A. gardineri* | Surface smooth, not hispid; fibre-bundles present, plumose and diverging | Slight reticula-tion with a few aspicular conn-ecting fibres; undifferent-iated axial/ extra-axial skeletons | Strongly rhabdose, spined on apical third, spines large and recurved (205-385× 11-21μm) | (1) Strongly rhabdose, spines on apical half, spines large and recurved (94-136×5-11μm); (2) strongly rhabdose, very slender, entirely smooth, fine point (84-156×1-2μm) | Well developed, brushes of ectosomal auxiliary styles/ anisoxeas often surrounding long subectosomal extra-axial styles/ anisoxeas (218-442×1-2μm) | Present, subectosomal extra-axial styles protrude through surface singly or in brushes (815-1050× 8-22μm) | Absent |
| *A. involutum* | Surface shaggy, large conules, not hispid; fibre-bundles present, promin-ent at surface, ascending in choanosome | No reticulation; undifferenti-ated axial/ extra-axial skeleton | Moderately to strongly rhabdose, spines on apical half, spines large and strongly recurved (224-370× 12-22μm) | Strongly rhabdose, spines on apical third, spines small (122-195× 5-11μm) | Vestigial, raphidiform oxeas perpendicular to surface but usually not formng brushes (450-640×5-7μm) | Present, single subectosomal extra-axial styles protrude through surface (1010-1390× 7-11μm) | Absent |
| *A. monticularis* | Surface shaggy, conulose, not hispid; fibre-bundles present, microcionid -like | No reticulation; undifferenti-ated axial/ extra-axial skeleton | Slightly rhabdose and subtylote, entirely smooth (290-518× 9-19μm) | Slightly rhabdose and subtylote, evenly spined, spines very small, granular and erect (132-275×2-9μm) | Absent | Present, single subectosomal extra-axial styles protrude through surface (620-960× 7-15μm) | Absent |
| *A. novae -caledoniensis* sp. nov . | Surface smooth, finely hispid; fibre-bundles present, plumose diverging | Slight reticula-tion with few aspicular conn-ecting fibres; undifferenti-ated axial/ extra-axial skeletons | Strongly rhabdose, spined only on extreme points, spines large and re-curved (275-400× 22-24μm) | Mod. Rhabdose, spines on apical half or 2/3, spines large and recurved (115-165× 8-10μm) | Vestigial, brushes of ectosomal auxiliary anisoxeas scattered but not surrounding any protruding spicules (455-565×2-5μm) | Absent | Absent |
| *A.samariensis* sp. nov. | Surface shaggy, bulbous, hispid; fibre-bundles present, plumose but with a few inter-connecting tracts | Very slight re-ticulation with sparse aspicular con-necting fibres; slightly more compressed in axis than periphery | Slightly rhabdose, spines mostly on base and apex, smooth elsewhere, spines large, recurved, hook-like (218-412× 9-18μm) | Slightly rhabdose, evenly spined but fewer spines below basal tyle, spines small and recurved (112-232×6-13μm) | Present, loose bundles of ectosomal auxiliary anis-oxeas surround subectosomal extra-axial spicules (225-775×2-6μm) | Present, single subectosomal extra-axial styles protrude through surface (920-2750× 8-26μm) | Absent |

TABLE 1. (*Cont.*)

| Species | Surface features & skeletal fibre-bundles | Skeletal reticulation & axial vs. extra-axial skeleton | Choanosomal principal spicules (spicule size) | Echinating spicules (spicule size) | Specialised ectosomal auxiliary skeleton (spicule size) | Subectosomal extra-axial spicules (spicule size) | Raphides (spicule size) |
|---|---|---|---|---|---|---|---|
| *A.spinosum* | Surface shaggy, conulose, not hispid; fibre-bundles present but with few inter-connecting tracts | Slight reticulation with only few connecting fibres; undifferentiated axial/ exra-axial skeleton | Slight to mod. rhabdose, entirely smooth (770-1085× 28-43µm) | Slight or no basal rhabd, slightly subtylote, evenly spined, spines very large, perpendicular (75-145×7-10µm); strongly rhabdose, slender, entirely smooth (90-185×5-12µm) | Absent | Absent | Present, singly and in trichodragmata (50µm long) |
| *A.villosa* | Surface very shaggy, conulose, not hispid; fibre-bundles present | No reticulation but adjacent echinating rhabdostyles may interconnect; undifferentiated axial/ extra-axial skeleton | Strongly rhabdose, usually completely smooth or with spines on apical half, spines very small, granular (235-370× 10-16µm) | Very strongly rhabdose, spines on apical half or entirely smooth, spines very small and granular (142-165×4-10µm) | Absent | Absent | Absent |
| **Raspailia (Raspaxilla) phakellina* | Surface slightly conulose; fibre-bundles present but confined to peripheral skeleton | Strongly reticulate axis; well differen-tiated reticulate axis, plumo-reticulate extra-axis, but skeleton dominated by plumose ascending fibres | Non-rhabdose, entirely smooth (550-900× 10-16µm) | Slightly rhabdose and subtylote, spines on apical two-thirds, spines small and erect (140-370×8-18µm) | Present, brushes of ectosomal auxiliary styles surrounding subectosomal extra-axial styles (450-650×2-3µm) | Present, single subectosomal extra-axial styles protrude through surface (1100-1450× 12-18µm) | Absent |
| **Endectyon (Hemectyon) hamatum* | Surface slightly corrugated; fibre-bundles absent | Strongly reticulate axis; compressed axial reticulation, radial extra-axial skeleton | Non-rhabdose, entirely smooth (270-515× 8-18µm) | Mod. rhabdose, spines only on extremities or apical third at most, spines large and very strongly recurved (120-150×5-10µm) | Vestigial, ectosomal auxiliary styles only found below surface, with rhabdostyles mostly surrounding the protruding choanosomal principal styles (220-275×2-3µm) | Absent | Absent |

REMARKS. This species has not been recorded since it was first described, and regrettably the holotype cannot be located in the AHF collections (Prof. G. Bakus, pers.comm.). Dickinson (1945) stated that it was a sister species of *R. inaequalis* Dendy, 1924 (which he also suggested belonged to *Echinaxia* in possessing ectosomal auxiliary oxeas, and which Hooper (1991) subsequently referred to *Raspailia* (*Raspaxilla*)), but this comparison is very superficial: *R. inaequalis* has a distinct, compressed axial and plumo-reticulate extra-axial region, possesses ectosomal specialisation, and has non-rhabdose choanosomal principal megascleres of distinctly different geometry than rhabdose echinating megascleres. Although incompletely described *A. cerebella* appears to be most similar to *A. flabellum* and *A. villosa* in having a reduced spiculation consisting only of choanosomal principal styles and echinating rhabdostyles, lacking any form of ectosomal auxiliary spicules or long subectosomal extra-axial spicules. Unlike both these species the larger choanosomal principal styles in *A. cerebella* do not appear to have a basal rhabd, which has presumably been secondarily modified.

**Aulospongus flabellum** Pulitzer-Finali, 1994
(Fig. 4, Table 1)

*Aulospongus flabellum* Pulitzer-Finali, 1994: 308, figs 38-39.

MATERIAL. HOLOTYPE. MSNG 48305 (not seen): North Kenya Banks, off Manda I., Kenya, 02°23'S, 41°04'E, 17.vi.1971, 110-170m depth.

DISTRIBUTION. Kenya, W Indian Ocean.

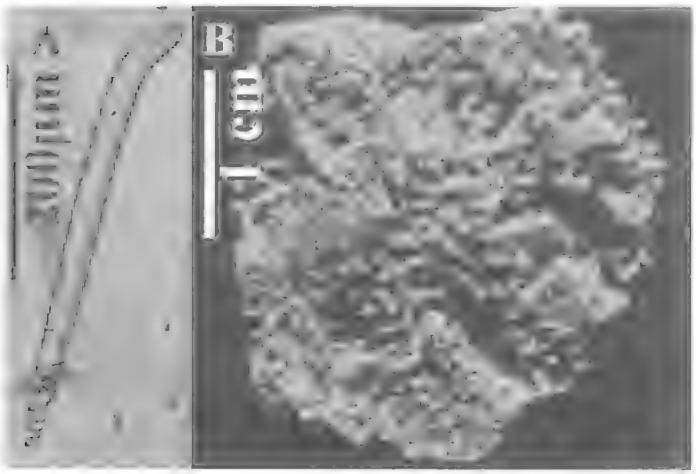



FIG. 3. *Aulospongus cerebella*. A, Holotype. B, Echinating rhabdostyle (figure modified from Dickinson, 1945).

DESCRIPTION. Thinly flabellate, planar, 45-55mm high, up to 4mm thick, with distict osculiferous and porous surfaces. Osculiferous surface with deep longitudinal ridges running the length of the sponge, with large oscules lying within grooves. Porous surface reticulate. Surface microscopically hispid. Colour unknown. Ectosomal skeleton unknown, although larger choanosomal principal spicules protrude through surface. Choanosomal skeleton unknown. Megascleres consist of choanosomal principal subtylostyles, completely smooth, with slight basal rhabd and subtylote swelling, straight shaft, fusiform points (340-570×16-34μm). Echinating rhabdostyles with large size range, larger ones subtylote, very slight or faint basal rhabd, straight shaft, with light spination on basal, distal and central portions, more-or-less aspinose between, smaller ones slightly subtylote, faint basal rhabd, straight shaft, evenly spinose, spines small (120-370×11.5-18.5μm). Subectosomal extra-axial and ectosomal auxiliary spicules apparently absent. Microscleres absent (Pulitzer-Finali, 1994).

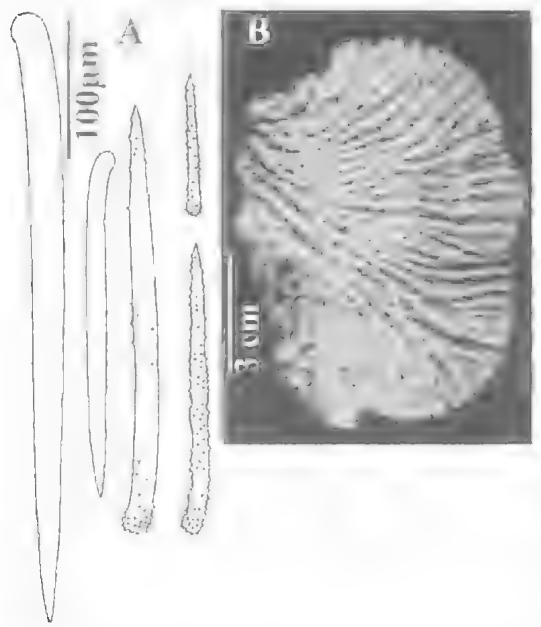



FIG. 4. *Aulospongus flabellum*. A, Choanosomal principal rhabdostyles (left), size range of echinating rhabdostyles (right). B, Holotype (figure modified from Pulitzer-Finali, 1993).

REMARKS. This species is very poorly known only from its original description. Unfortunately type material is not available from the MSNG, and its apparent affinities can only be speculated from Pulitzer-Finali's (1994) incomplete description and illustrations. In the absence of a skeletal description its placement is not certain, although *Aulospongus* may be correct given that both choanosomal principal and echinating styles show various degrees of basal rhabds, indicating possible common origin.

In growth form *A. flabellum* shows an uncanny superficial resemblance to *Echinodictyum mesenterinum* (also known from E Africa; Hooper, 1991), including the possession of differentiated osculiferous and porous surfaces. Assuming that Pulitzer-Finali's (1994) description of the spicule complement is complete for *A. flabellum*, it shows greatest similarities to *A. cerebella* and *A. tubulatus* in spicule diversity, and in particular to the latter species in geometry of the larger, smooth choanosomal principal rhabdostyles (nearly identical size and shape). The two species differ in the diversity and size of smaller echinating rhabdostyles, with *A flabellum* having two categories and the larger ones nearly twice the size of those in *A. tubulatus* (120-370×11-18μm versus 109-126×5-10μm, respectively).

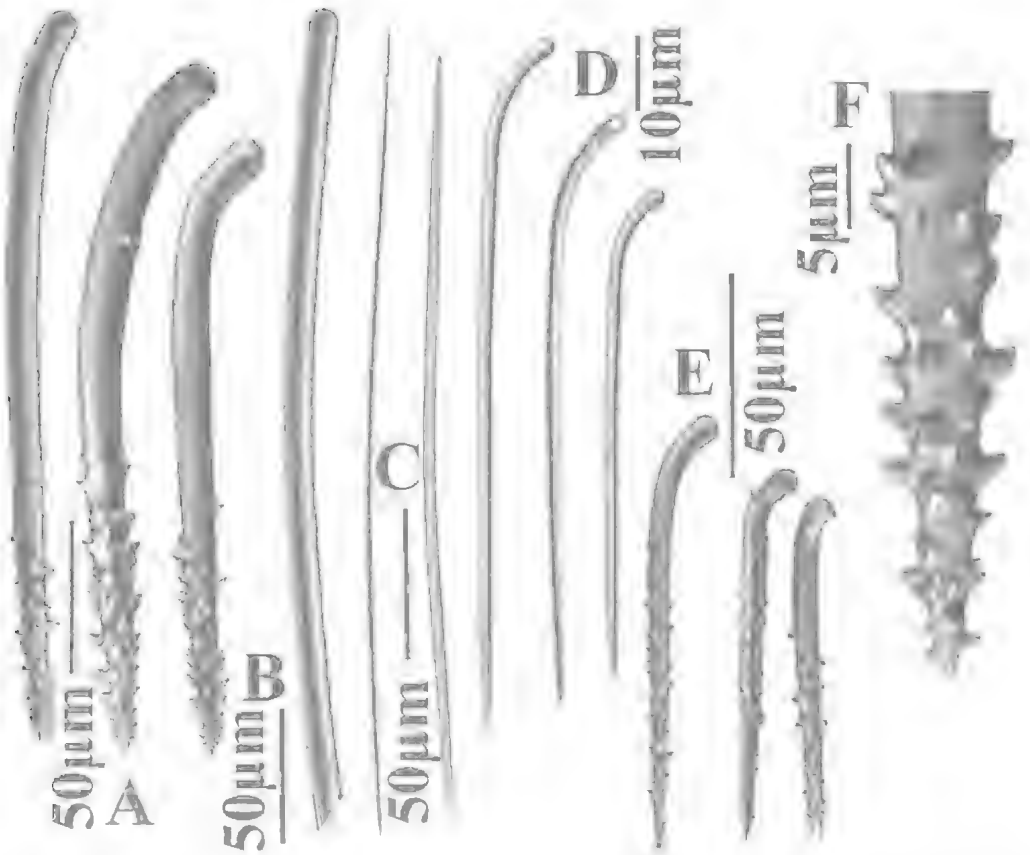



FIG. 5. *Aulospongus gardineri*. A, Choanosomal principal rhabdostyles. B, Subectosomal extra-axial style. C, Ectosomal auxiliary styles/anisoxeas. D, Third category of rhabdostyles. E, Echinating rhabdostyles. F, Apical spination on choanosomal principal rhabdostyle.

**Aulospongus gardineri**
(Dendy, 1922)
(Figs 5-6, Table 1)

*Plumohalichondria gardineri* Dendy, 1922: 87, pl. 2, fig. 9, pl. 15, fig. 4a-d; Vacelet & Vasseur, 1971: 83.
*Aulospongus gardineri*; Hooper, 1991: 1309, fig. 67e-h; van Soest, 1994: 72.
Not *Hemectyonilla gardineri*; Lévi & Lévi, 1983: 950, pl. 2, figs 2,3,5, fig. 14.

MATERIAL. HOLOTYPE. BMNH1921.11.7.74: Amirante, coll. 'Sealark', 18.x.1905, 40-88m depth.

DISTRIBUTION. Amirante, Tulear, Madagascar, Seychelles, Indian Ocean.

DESCRIPTION. Growth form erect lobate, lamellate or bulbous. Surface nearly smooth, granular. Colour dull yellowish-grey in ethanol. 'Raspailiid ectosomal skeleton' moderately well developed, with ectosomal auxiliary styles forming thick surface brushes, although not always associated with the protruding long subectosomal extra-axial styles, the latter also lying in tracts parallel to fibres and protruding through the surface in radiate tufts. Choanosomal skeleton consists of close-set, thick, plumose fibre-bundles diverging and branching towards the periphery, occasionally interconnected by small aspicular fibres, heavily echinated by both smaller rhabdostyles and smooth rhabdostyles, nearly all pointing outwards. Fibre-bundles only sparsely cored by choanosomal principal rhabdostyles whereas all three size classes of rhabdostyles project nearly at right angles to fibres, together producing much more bulbous fibre-bundles than other species. Megascleres consist of 3 size classes of rhabdostyles: larger choanosomal principal rhabdostyles with prominently curved and subtylote basal rhabd, large recurved spines confined mainly to the apical (pointed) third or half of the spicule, smooth base occasionally with few small spines

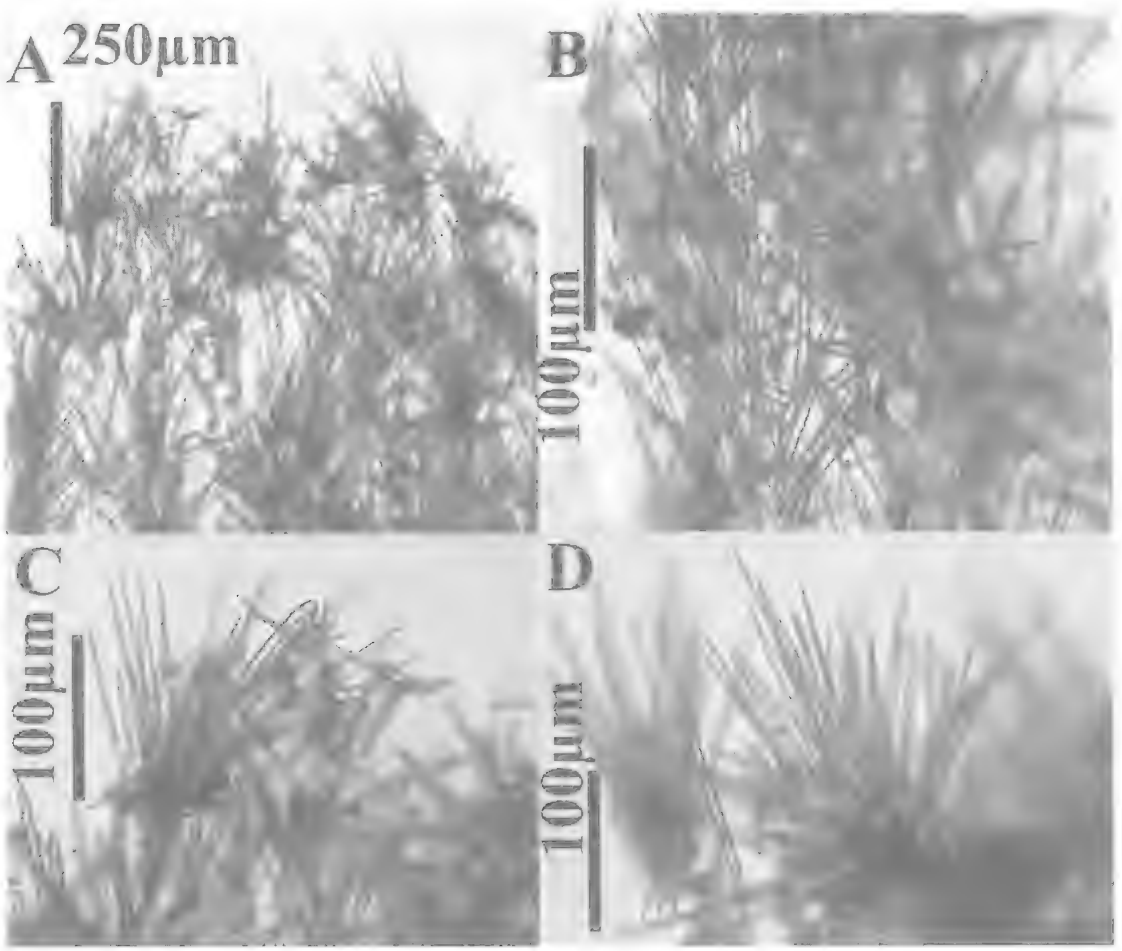



FIG. 6. *Aulospongus gardineri*. A, Peripheral skeleton. B, Choanosomal fibre. C, Ectosomal skeleton. D, Ectosomal auxiliary spicule bundle.

(205-385×11-21µm); smaller echinating rhabdostyles with very strong basal rhabd, base occasionally spined, spines more evenly dispersed or concentrated on apical half, spines relatively large, recurved (94-136×5-11µm); third class of smooth rhabdostyle long, very slender, with strong basal rhabd, subtylote base, completely smooth, tapering to a fine point (84-156×1-2µm). Subectosomal extra-axial styles or anisoxeas long, smooth, slightly curved near base, evenly rounded base (815-1050× 8-22µm). Ectosomal auxiliary styles/ anisoxeas straight or slightly curved, usually with one blunt or tornote end, sometimes tapering at both ends (218-442×1-2µm). Microscleres absent.

REMARKS. Lévi & Lévi's (1983) specimen from deeper waters off New Caledonia, described as *A. gardineri*, is not conspecific with Dendy's (1922) material from Amirante, although the two appear to be related in some of their features. The former material is described below as a new species, *A. novaecaledoniensis* sp. nov. In *A. gardineri* larger subectosomal extra-axial spicules are present and are surrounded by bundles of ectosomal auxiliary styles/anisoxeas (absent in *A. novaecaledoniensis*); there is a unique third category of rhabdostyle (absent in the latter species); spination on rhabdostyles extends at least 25% (or more) along apical end of spicule (confined to extreme apex only in the latter species); spicule dimensions are generally smaller (see Table 1); and there are many more plumose fibre-bundles with rhabdostyles projecting/echinating fibres nearly at right angles (fewer projecting rhabdostyles and echinating at more acute angles in the latter species).

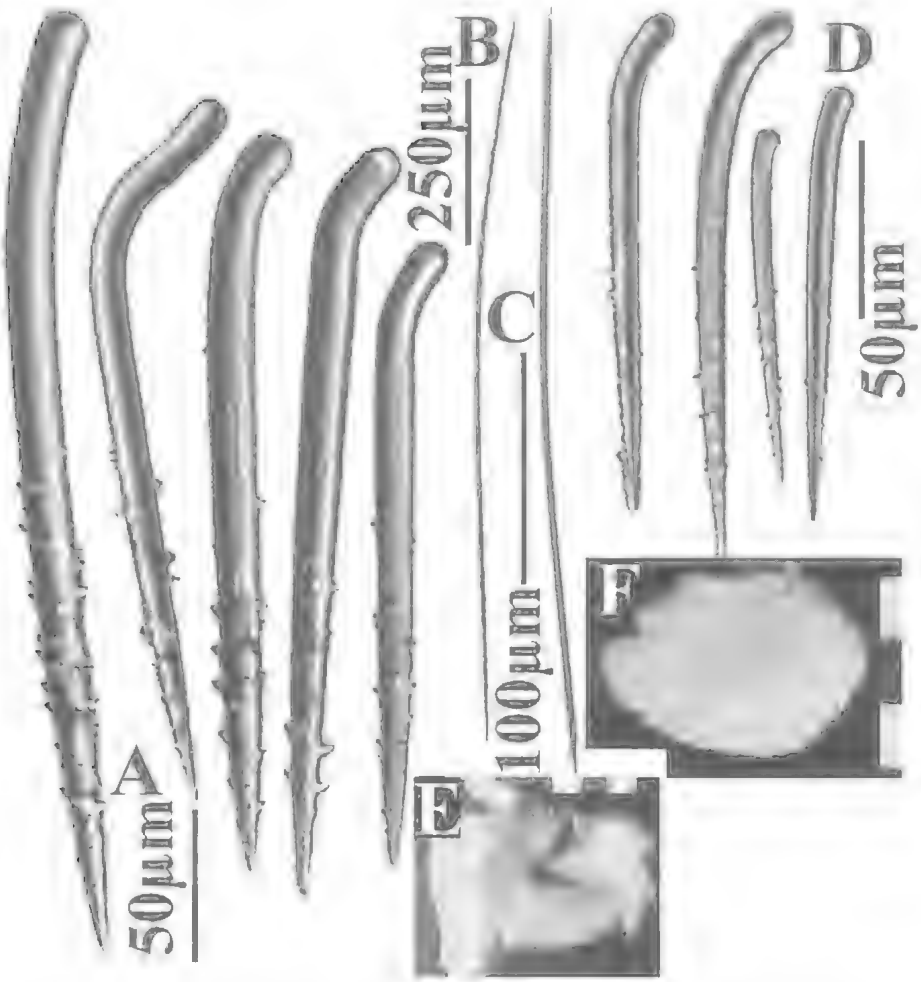



FIG. 7. *Aulospongus involutum*. A, Choanosomal principal rhabdostyles. B, Subectosomal extra-axial anisoxea. C, Ectosomal auxiliary anisoxea. D, Echinating rhabdostyles. E, Holotype (scale 3cm). F, 'John Murray' specimen (scale 3cm).

In rhabdostyle geometry this species is also similar to *A. involutum* (which prompted Burton (1959) to synonymise the two), but they differ in many other respects (fibre characteristics, choanosomal and ectosomal skeletal structure, spicule sizes and spicule diversity (see Table 1)), which Lévi & Lévi (1983) and Hooper (1991) indicated they were distinct species. *Aulospongus gardineri* is unusual in having a macroscopically smooth surface (although microscopically it is hispid from the protruding subectosomal extra-axial styles), and in possessing of a third category of rhabdostyle (similar only to *A. spinosum* in this respect, although the two species differ in virtually all other characters; Table 1).

**Aulospongus involutum** (Kirkpatrick, 1903)
(Figs 7-8, Table 1)

*Stylostichon involutum* Kirkpatrick, 1903: 250, pl. 5, fig. 16, pl. 6, fig. 17a-e.
*Hemectyonilla involutum*; Burton, 1959: 254.
*Aulospongus involutum*; Pultizer-Finali, 1993: 308-309; Hooper, 1991: 1307, fig. 66a-f.

MATERIAL. HOLOTYPE. BMNH1902.11.16.33 (fragment MNHN LBIM DCL61): Cone Point, Natal, South Africa, 68m depth. OTHER MATERIAL. BMNH1936.3.4.118: Gulf of Aden, 11°56-57'N, 50°35-39'E, coll. 'John Murray', 12.x.1933, 37m depth.

DISTRIBUTION. Natal, Zanzibar, Kenya, Gulf of Aden, South Arabian coast and Arabian Gulf, Indian Ocean.

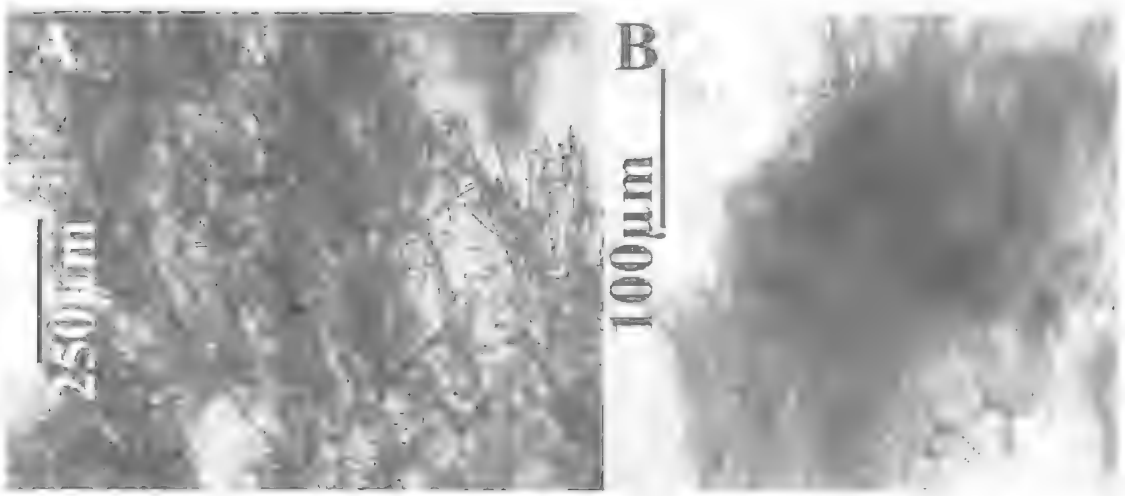



FIG. 8. *Aulospongus involutum*. A, Choanosomal skeleton. B, Ectosomal skeleton.

DESCRIPTION. Growth form plate-like, vasiform with very thick lamellae. Surface shaggy, conulose. Colour brown in ethanol. 'Raspailiid ectosomal skeleton' reduced, composed of raphidiform ectosomal auxiliary anisoxeas/oxeas perpendicular to the surface, not usually forming brushes, and extremely long, thin subectosomal extra-axial styles or anisoxeas protruding through the surface. Choanosomal skeleton exclusively plumose, lacking any axial compression or obvious differentiation between axial and extra-axial regions, although peripheral skeleton tracts form prominent tufts at the surface, producing relatively large conules. Larger rhabdostyles form plumose tufts along fibre-bundles, which are radial, microcionid-like, plumose, and heavily echinated by smaller rhabdostyles. Megascleres consist of larger choanosomal principal rhabdostyles with moderate to strong basal rhabd, subtylote and completely smooth bases, smooth for most of the distal end of the shaft, with only a few large, strongly recurved spines on the apical third of spicules (224-370×12-22µm). Smaller echinating rhabdostyles with strong basal rhabd, slightly subtylote and completely smooth bases, small spines restricted to apical half of spicules (122-195×5-11µm). Subectosomal extra-axial anisoxeas long, smooth, slightly curved at centre (1010-1390×7-11µm). Ectosomal auxiliary oxeas or anisoxeas are raphidiform, straight or very slightly curved (450-640×5-7µm). Microscleres absent.

REMARKS. Kirkpatrick (1903) described sigma microscleres present in this species, and a few were seen in spicule preparations made from the holotype, but these are obviously contaminants and were not seen in histological sections. Rhabdostyles of *A. involutum* have a similar geometry to those of *A. gardineri*, although they are not synonyms as suggested by Burton (1959) (Hooper, 1991), with *A. involutum* lacking the third category of rhabdostyle unique to *A. gardineri*, and also lacking aspicular fibres present in *A. gardineri* and *A. tubulatus*. Subsequent records of this species from E Africa by Burton (1959) and Pulitzer-Finali (1993) agree very closely with those of the specimens re-examined here. Pulitzer-Finali (1993) stated that subectosomal extra-axial spicules were styles, but these are clearly anisoxeote.

**Aulospongus monticularis**
(Ridley & Dendy, 1886)
(Figs 9-10, Table 1)

*Axinella monticularis* Ridley & Dendy, 1886: 481; 1887: 185, pl. 38, fig. 5.
*Aulospongus monticularis*; Hallmann, 1917: 373; Hooper, 1991: 1307, fig. 65a-e.
*Microciona monticularis*; Burton, 1956: 132.
*Aulospongiella monticularis*; Burton, 1956: 141.

MATERIAL. HOLOTYPE. BMNH1887.5.2.20: São Vicente Harbour, Cape Verde I., coll. 'Challenger', -.vii.1873, 14-40m depth. PARATYPE. BMNH-1887.5.2.273: same locality.

DISTRIBUTION. Cape Verde I., N Atlantic, São Vicente, W Africa.

DESCRIPTION. Growth form massive, bulbous-encrusting. Surface shaggy, conulose.

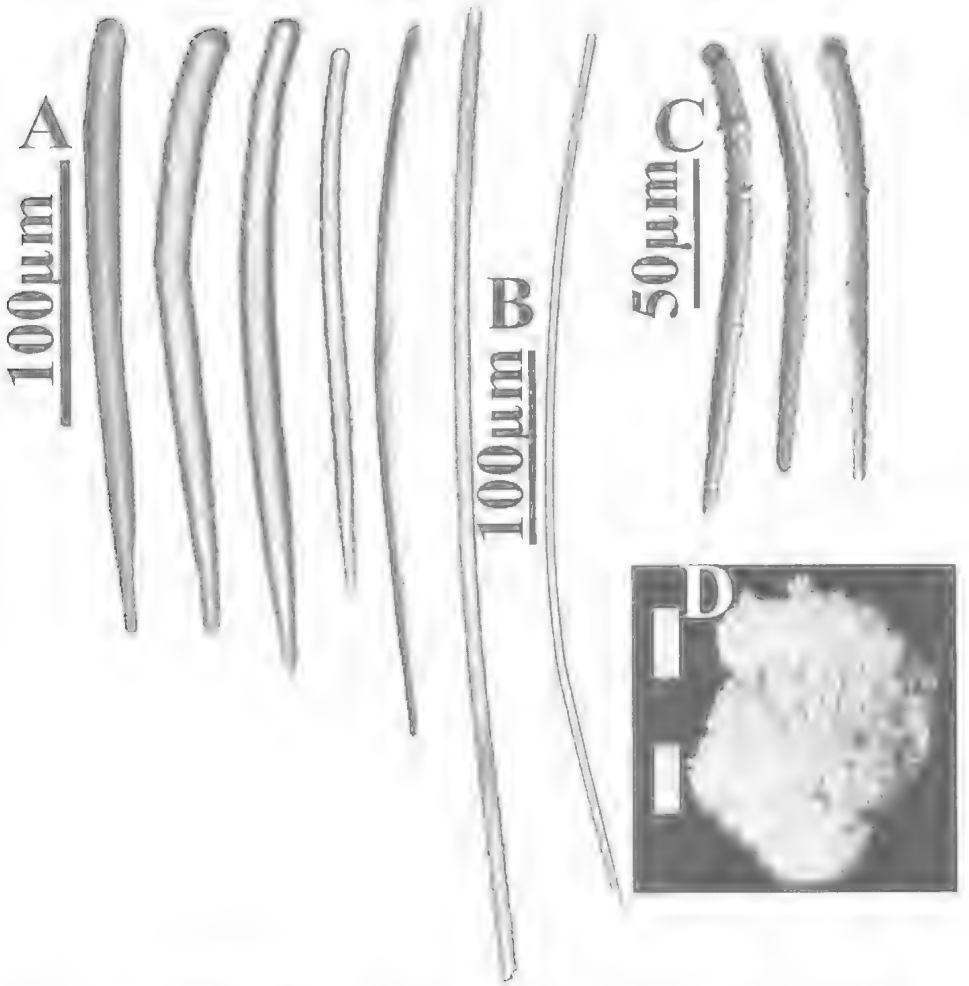



FIG. 9. *Aulospongus monticularis*. A, Choanosomal principal rhabdostyles. B, Basal end of subectosomal extra-axial styles. C, Echinating rhabdostyles. D, Holotype (scale 3cm).




FIG. 10. *Aulospongus monticularis*. A, Microcionid-like choanosomal skeleton arising from basal detritus. B, Peripheral skeleton.

Colour yellowish-grey in ethanol. 'Raspailiid ectosomal skeleton' absent, although larger subectosomal extra-axial styles occasionally protrude through surface. Choanosomal skeleton microcionid-like, composed of large, non-anastomosing, plumose fibre-bundles, without any trace of axial compression or differentiation between axial and extra-axial regions. Ascending fibre-bundles arise from detritus-encrusted basal skeleton, and foreign particles also incorporated into choanosomal skeleton. Ascending fibre-bundles cored and echinated by both categories of rhabdostyles, although larger rhabdostyles comprise most of the coring spicules, as well as protruding through fibres in plumose bundles. Megascleres consist of larger choanosomal principal rhabdostyles with only slight basal rhabd, completely smooth, rounded or slightly subtylote bases (290-518×9-19μm). Smaller echinating rhabdostyles more-or-less evenly spined, microcionid-like, slightly curved at centre, with very small, granular, erect spines, only slight basal rhabd and slight to moderate subtylote basal swelling (132-275×2-9μm). Subectosomal extra-axial styles slightly curved near basal end, with slightly subtylote bases and very long tapering points (620-960×7-15μm). Ectosomal auxiliary spicules absent. Microscleres absent.

REMARKS. This species is similar to *A. involutum* in having long subectosomal extra-axial spicules protruding through the surface, which are not surrounded by ectosomal auxiliary spicules, as typical for most raspailiids. It differs from *A. involutum* in lacking rhaphidiform ectosomal auxiliary spicules completely, as well as in other important characters such as the geometry, small size and vestigial spination of rhabdostyles (Table 1). It should also be compared to *A. villosa* and *A. cerebella* which also lack any ectosomal specialisation, differing from *A. villosa* in having completely smooth larger rhabdostyles (generally longer than those of *A. villosa*), microcionid-like, evenly spined smaller rhabdostyles (partially spined in *A. villosa*), and a bulbous growth form (bushy growth form in *A. villosa*) (see Table 2). Rhabdostyle morphology differs substantially between *A. monticularis* and *A. cerebella*: larger rhabdostyles are of similar size, but those in the latter species have only a slight basal rhabd; smaller rhabdostyles are evenly spined in both species but about half the size in *A. monticularis*.

**Aulospongus novaecaledoniensis** sp. nov.
(Figs 11-12, Table 1)

*Hemectyonilla gardineri*; Lévi & Lévi, 1983: 950, pl. 2, figs 2,3,5, fig. 14.

ETYMOLOGY. For the type locality.

MATERIAL. HOLOTYPE. MNHN LBIM DCL2941: Havannah, New Caledonia, 22°17'S, 167°14'E, coll. 'Vauban' (stn.DP36), 24.v.1978, 425-430m depth. PARATYPE. MNHN LBIM DCL2940: same locality, 22°19'S, 167°11'E, 300-315m depth.

DISTRIBUTION. New Caledonia.

DESCRIPTION. Growth form massive, tubular. Surface finely hispid, generally smooth apart from several large surface conules, each surmounted by a terminal oscule. Colour in ethanol brownish ocre with slight pinkish tinge. 'Raspailiid ectosomal skeleton' moderately well developed, with ectosomal auxiliary styles forming thick surface brushes, although not associated with any subectosomal extra-axial spicules (the latter absent completely from this species). Choanosomal skeleton essentially plumose, consisting of close-set, thick, ascending fibre-bundles, diverging and branching towards the periphery. Ascending fibres moderately heavily cored by larger rhabdostyles, forming mainly axial bundles within fibres and only slightly plumose tracts of single rhabdostyles protruding through fibres, with their points ascending towards the surface. Smaller rhabdostyles concentrated mainly at the base of main ascending fibres. Ascending fibres interconnected by few, aspicular, transverse fibres sparsely echinated by smaller rhabdostyles. Megascleres consist of larger choanosomal principal rhabdostyles with variably developed smooth basal rhabds, ranging from nearly straight to prominently rhabdose, with basal rhabd occupying between 15-40% of spicule length, shaft smooth except for a few (4-12) large recurved spines located only on the extreme apical (pointed) end of the spicule (275-415×19-26μm). Smaller echinating rhabdostyles with only moderate basal rhabd (sometimes slight), base usually subtylote, smooth or occasionally with a few spines, shaft with spines concentrated on apical half (not merely confined to extreme point of spicule as for larger rhabdostyles), spines relatively large, recurved (122-195×7-13μm). Subectosomal extra-axial megascleres absent. Ectosomal auxiliary anisoxeas (occasionally styles) large, slightly curved at the centre, usually with one blunt or tornote end, sometimes tapering

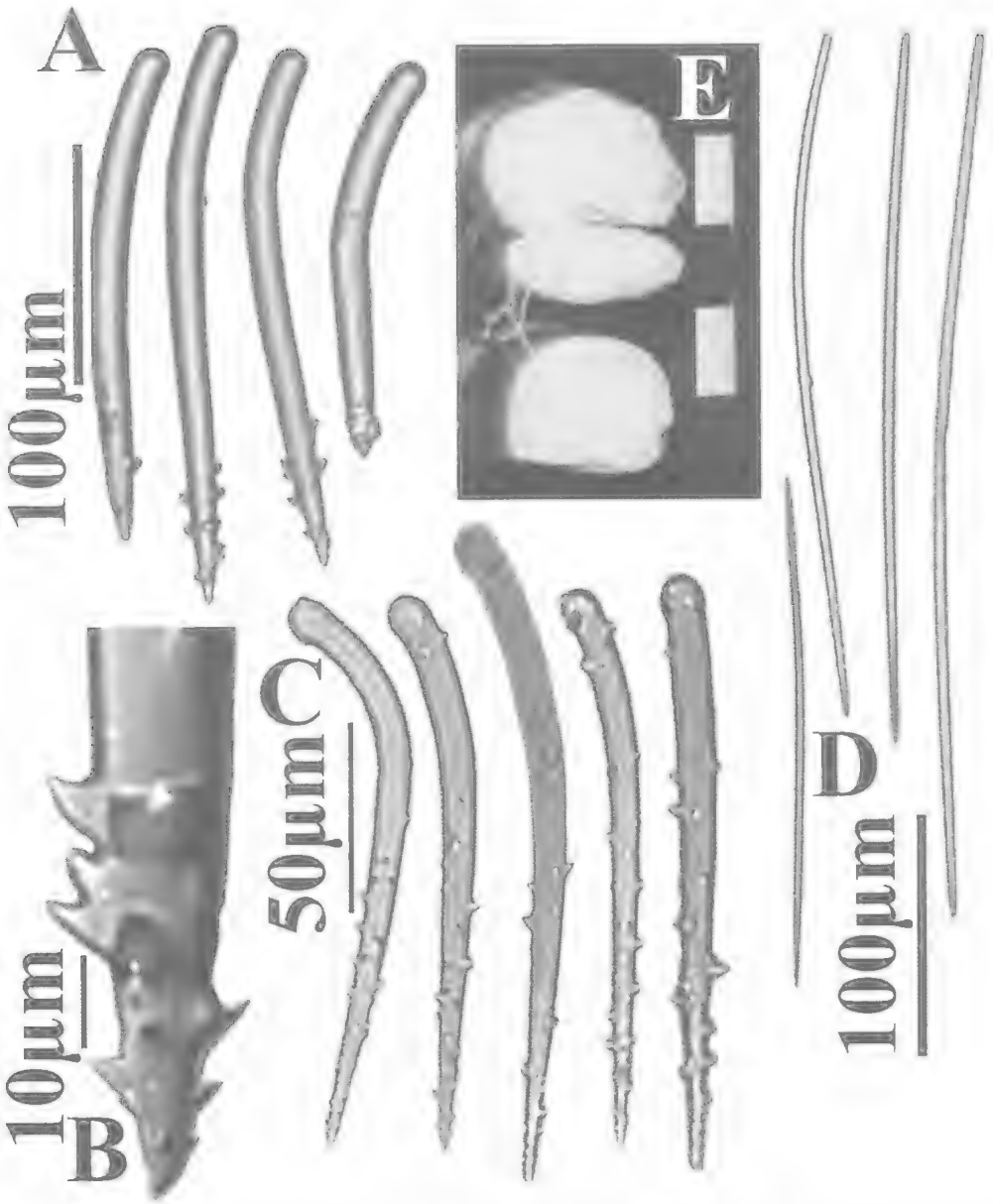



FIG. 11. *Aulospongus novaecaledoniensis* sp. nov. A, Choanosomal principal rhabdostyles. B, Apical spines on choanosomal principal rhabdostyle. C, Echinating rhabdostyles. D, Ectosomal auxiliary anisoxeas. E, Holotype and fragment (scale 3cm).

at both ends, rarely symmetrical sharply pointed (445-585×3-6µm). Microscleres absent.

REMARKS. Lévi & Lévi (1983) initially referred their material from New Caledonia to Dendy's (1922) species *A. gardineri* (from Amirante, Indian Ocean), based on inferred similarities in their respective growth forms, pattern of spination and geometry of both smaller and larger rhabdostyles. However, *A. novaecaledoniensis* sp. nov. lacks the third category of rhabdostyle unique to *A. gardineri*; lacks larger subectosomal extra-axial styles/anisoxeas completely; spines on the larger rhabdostyles are much more sparse and confined only to the extreme apex (point) of spicules; and spicule

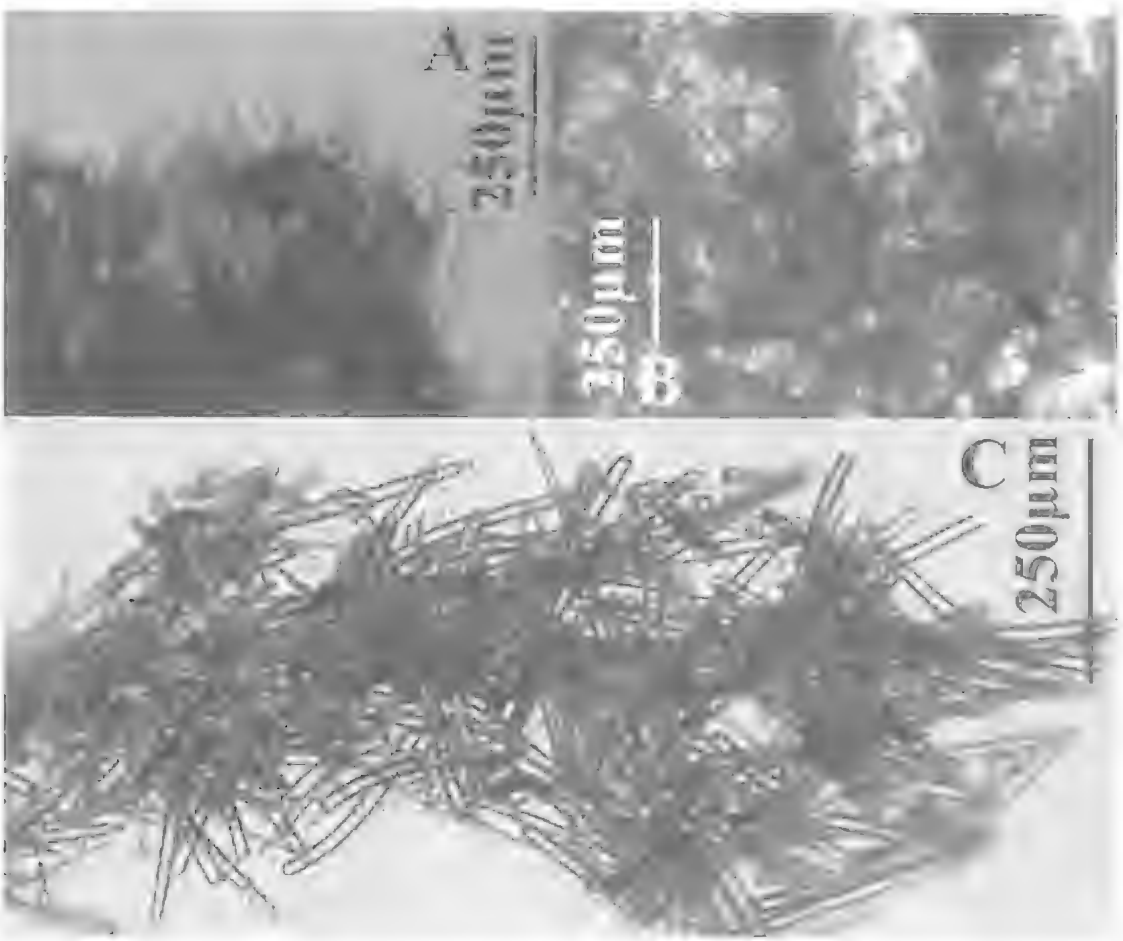



FIG. 12. *Aulospongus novaecaledoniensis* sp. nov. A, Peripheral skeleton. B, Choanosomal skeleton. C, Choanosomal fibre bundle.

dimensions are substantially larger than those of *A. gardineri* (Table 1). More subjectively, this species also has much more compact fibre-bundles than does *A. gardineri*, the former having rhabdostyles mainly confined to the axis of fibres and only slightly projecting through the fibres as single spicules, pointing towards the surface, whereas the latter species has plumose bundles of rhabostyles projecting nearly at right angles to fibres, forming prominently plumose tracts. Nevertheless, the two species are related by these features.

**Aulospongus samariensis** sp. nov.
(Figs 13-16, 36A-B, Tables 1-2)

*Raspailia* (*Raspaxilla*) sp.: Silvestri, Zea & Duque, 1994: 21.

ETYMOLOGY. Named for the holotype locality of Santa Marta.

MATERIAL. HOLOTYPE. ICN-MHM(Po)0171: Nenguange Bay, 'Piedra Ahogada', Magdalena Department, Colombia, Caribbean Sea, 11°25'N, 75° 10'W, 26m depth, 27-vi-1983, coll. Sven Zea (PEB-013), SCUBA, Second Botanic Expedition, on coral rubble, reef base. PARATYPES. QMG304501: Bahia de Nenguange, Santa Marta, Colombia, Caribbean Sea, 26m depth, 27.vi.1983, coll. S. Zea, SCUBA, coral rubble. QMG313310, G313311: Dairy Bull, Discovery Bay, Jamaica (Caribbean Sea), 18°28'N, 77° 24'W, coll. H. Lehnert, SCUBA using trimix (see Lehnert & van Soest, 1996), 90m depth (ref. no. J96/41, 28.vi.96). INV-POR-0455: 'Punta de Betín', Santa Marta Bay, Magdalena Department, Colombia, Caribbean Sea, 12m depth, 10.ix.1982, coll. S. Zea (PSM229), SCUBA, on dead sides of coral head, patch reef. INV-POR-0456: same locality, 6m depth, 15.xi.1982, metamorphic rock, rocky shore (PSM239).

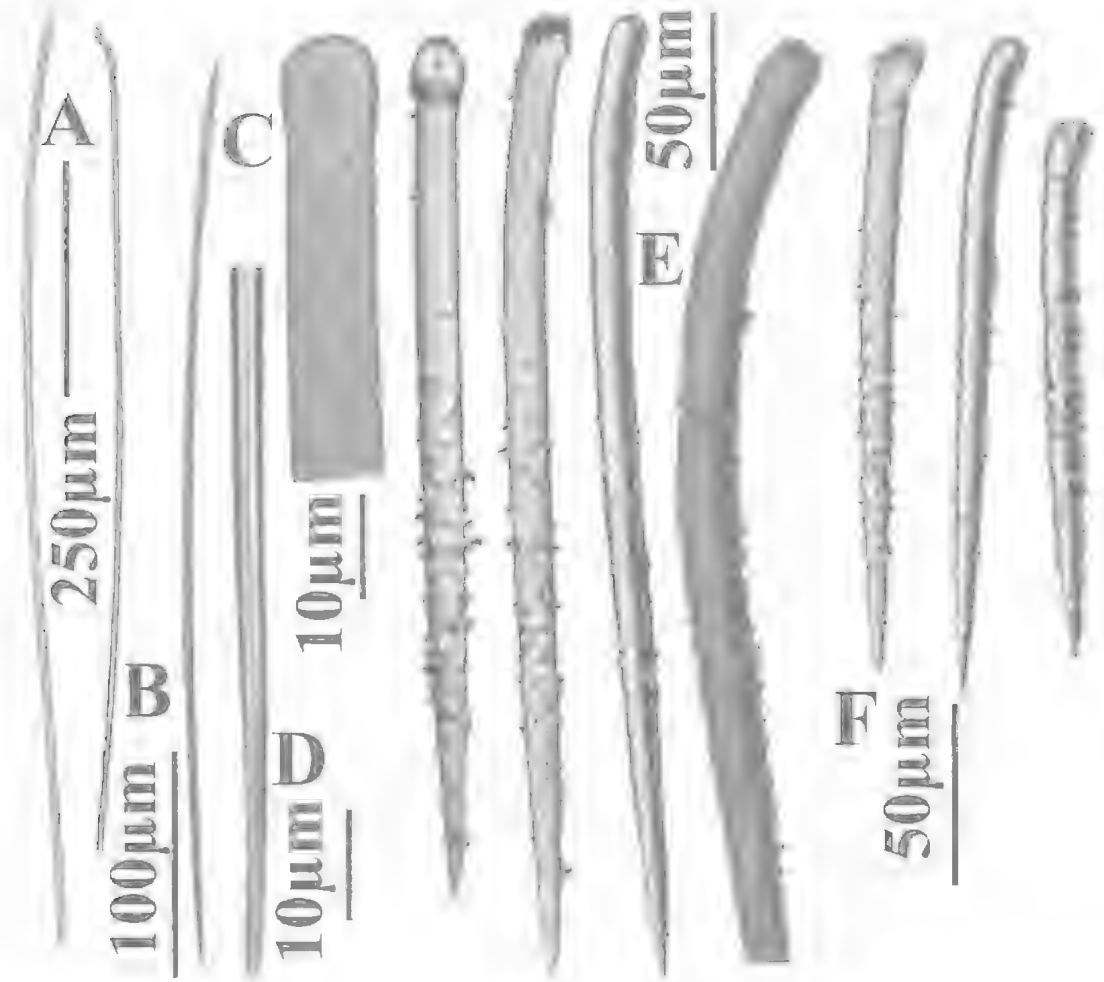



FIG. 13. *Aulospongus samariensis* sp. nov. (W Caribbean population, paratype QMG304501) A, Subectosomal extra-axial styles/subtylostyles. B, Ectosomal auxiliary anisoxea. C, Base of subectosomal extra-axial subtylostyle. D, Apex of subectosomal extra-axial style. E, Choanosomal principal rhabdostyles. F, Echinating rhabdostyles.

DISTRIBUTION. Santa Marta region, W Caribbean, Jamaica, E Caribbean

DESCRIPTION. *Growth form.* Erect, stalked, vaguely cylindrical, club-shaped, slightly bushy, 5-12cm high, 0.5-2.5cm diameter, with several small irregular bulbous lobate branches up to 0.7-3cm diameter, partially fused and becoming more swollen at their tips. Protruding fibre-bundles from underlying skeleton producing a shaggy appearance at the surface, superficially resembling *Pandaros acanthifolium* (Duchassaing & Michelotti, 1864) (Microcionidae). Fibre-bundles at the centre of the sponge are dense, narrow, winding and branching, with the longitudinal axis produced by fusion of fibres clearly dominant. Numerous short thin branches located towards periphery which subdivide repeatedly.

*Surface.* Shaggy, slightly bulbous, prominent hispid ridges running longitudinally, subparallel along branches, with individual ridges composed of smaller lamellae or tuberculate conules; valleys between ridges thickly collagenous, smooth, with ectosome stretched between ridges and towards apex of branches forming a shiny surface in life, or with deep valleys when ectosome collapses out of water.

*Colour.* Brownish yellow (Munsell 5YR 6/6) to dark brown alive (NCG 23 (raw amber), 36 (amber) to 219 (sepia)). Apical branch tips with

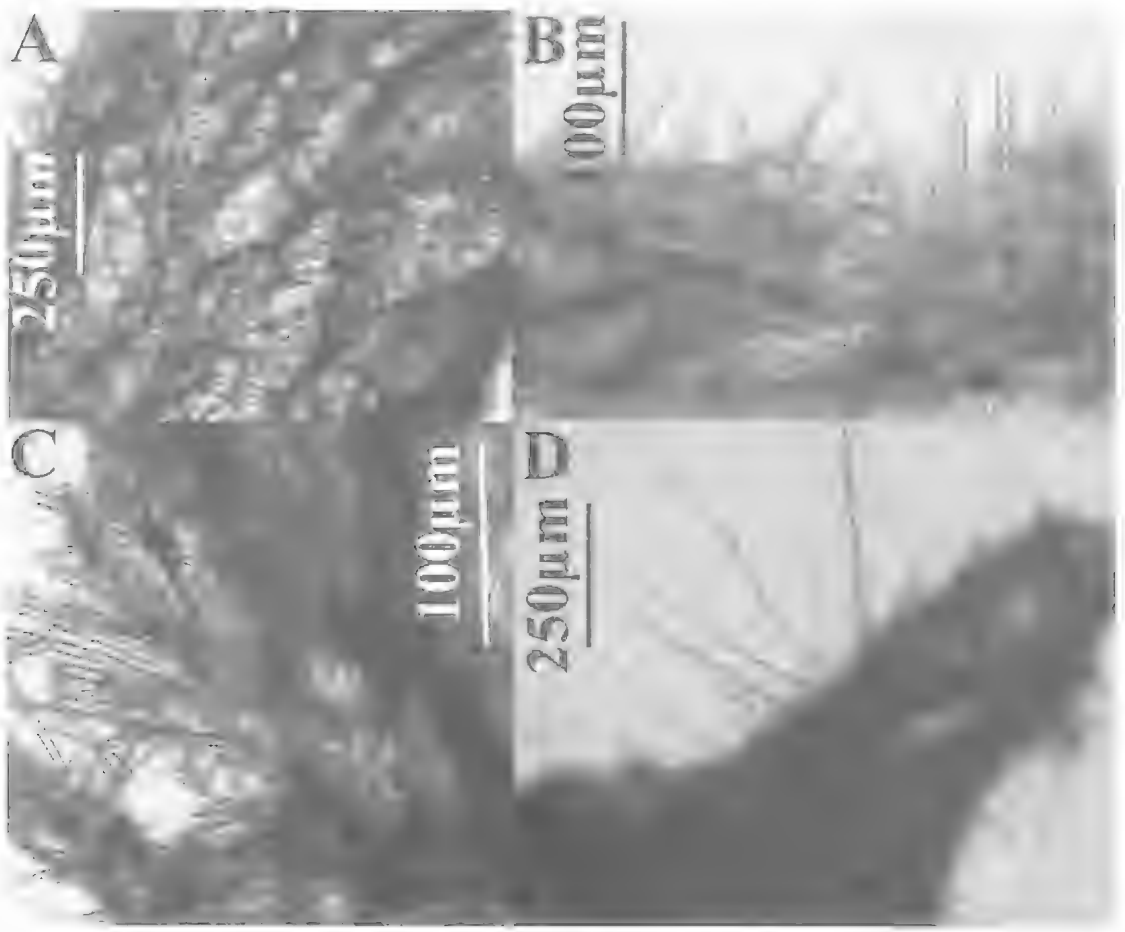



FIG. 14. *Aulospongus samariensis* sp. nov. (W Caribbean population, paratype QMG304501) A, Choanosomal skeleton. B, Peripheral skeleton. C, Peripheral fibre-bundles. D, Ectosomal skeleton.

mustard yellow tinge (NCG 24 (buff)). Preserved specimens evenly brown.

*Oscules.* Small,<0.5-2mm diameter, inter-dispersed in cavities on produced by folding of surface ridges, collapsing out of water.

*Texture.* Firm, compressible, with stiff, flexible, elastic branches.

*Ectosomal skeleton.* Ectosome with thick, organic, heavily collagenous matrix up to 200µm thick. 'Raspailiid ectosomal skeleton' present consisting of clusters of loose ectosomal auxiliary anisoxeas, forming bouquets on the surface conules, surrounding the usually single, long subectosomal extra-axial styles at the point they protrude through the surface. Occasional plumose bundles of larger choanosomal principal rhabdostyles also protrude through the surface (on conules), and individual rhabdostyles form an evenly spaced palisade in between surface conules.

*Choanosomal skeleton.* Skeletal structure predominantly plumose, only very faintly more compressed, slightly reticulate, in axis than in periphery. Axial skeletal reticulation composed of fibre-bundles more-or-less amalgamated into large tracts, sparsely interconnected by collagen and/or aspicular or paucispicular 'secondary fibres'. Fibres in peripheral skeleton with very few reticulate elements, disappearing closer to the surface, with ascending fibre-bundles diverging and forming discrete conules at the surface. Primary reticulate fibres and ascending fibres fully cored by larger rhabdostyles, protruding through fibres at obtuse angles, and heavily echinated by both smaller and larger rhabdostyles forming heavy plumose tracts, producing clumps of spicules particularly at fibre

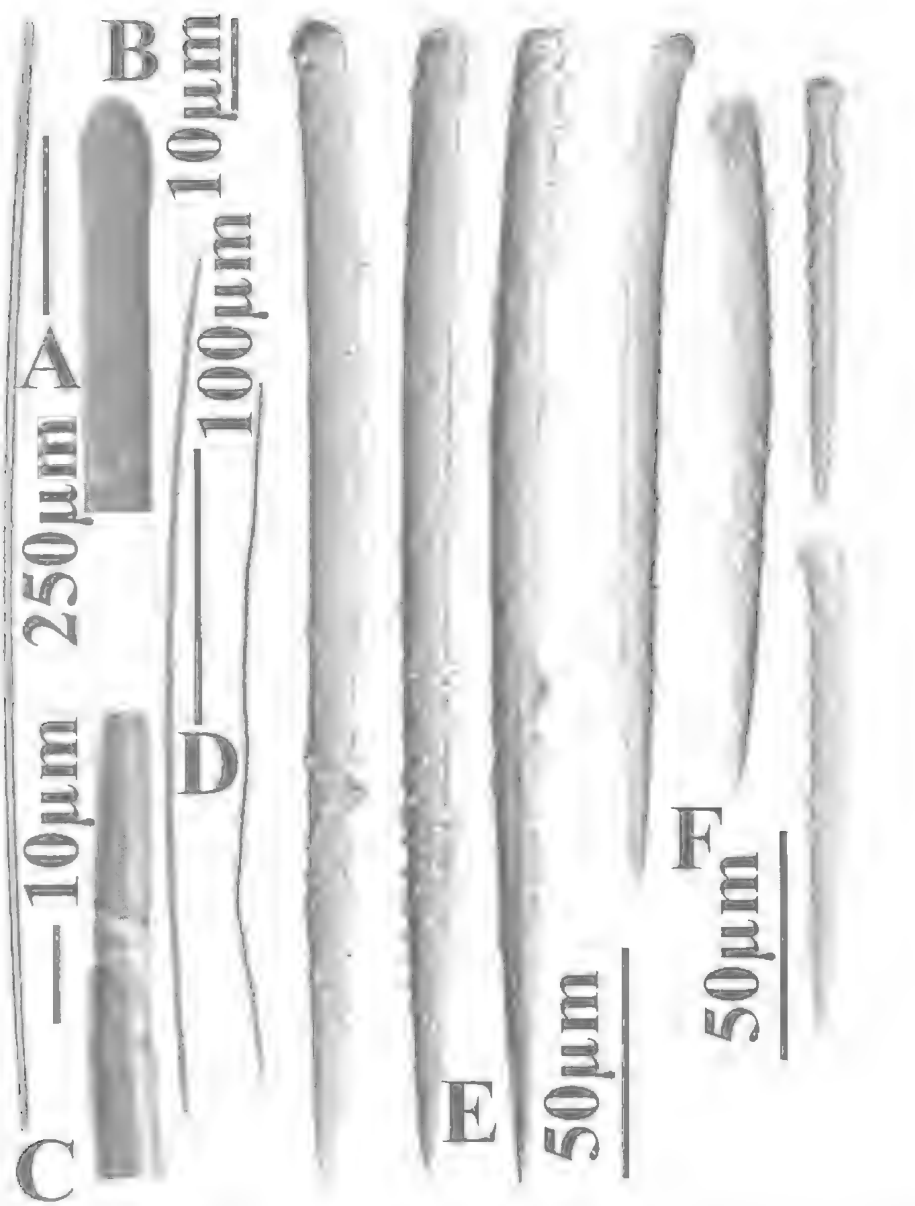



FIG. 15. *Aulospongus samariensis* sp. nov. (E Caribbean population, paratype QMG313310) A, Subectosomal extra-axial subtylostyle. B, Base of subectosomal extra-axial subtylostyle. C, Base of ectosomal auxiliary anisoxea. D, Ectosomal auxiliary anisoxeas. E, Choanosomal principal rhabdostyles. F, Echinating rhabdostyles.

nodes, with larger rhabdostyles dominating tracts and smaller ones interdispersed between them. Choanosomal principal rhabdostyles appear larger in the periphery than in axial regions of the skeleton. Long subectosomal extra-axial subtylostyles have their bases embedded in spongin fibres, forming sparse radial tracts protruding a long way through the surface Collagen between the fibres is light, generally aspicular, although multispicular tracts of subectosomal extra-axial styles run along the longitudinal axis of branches towards the surface, more-or-less parallel to (and external of) spongin fibres. Meshes between fibre are relatively small, close-set, 150-250µm

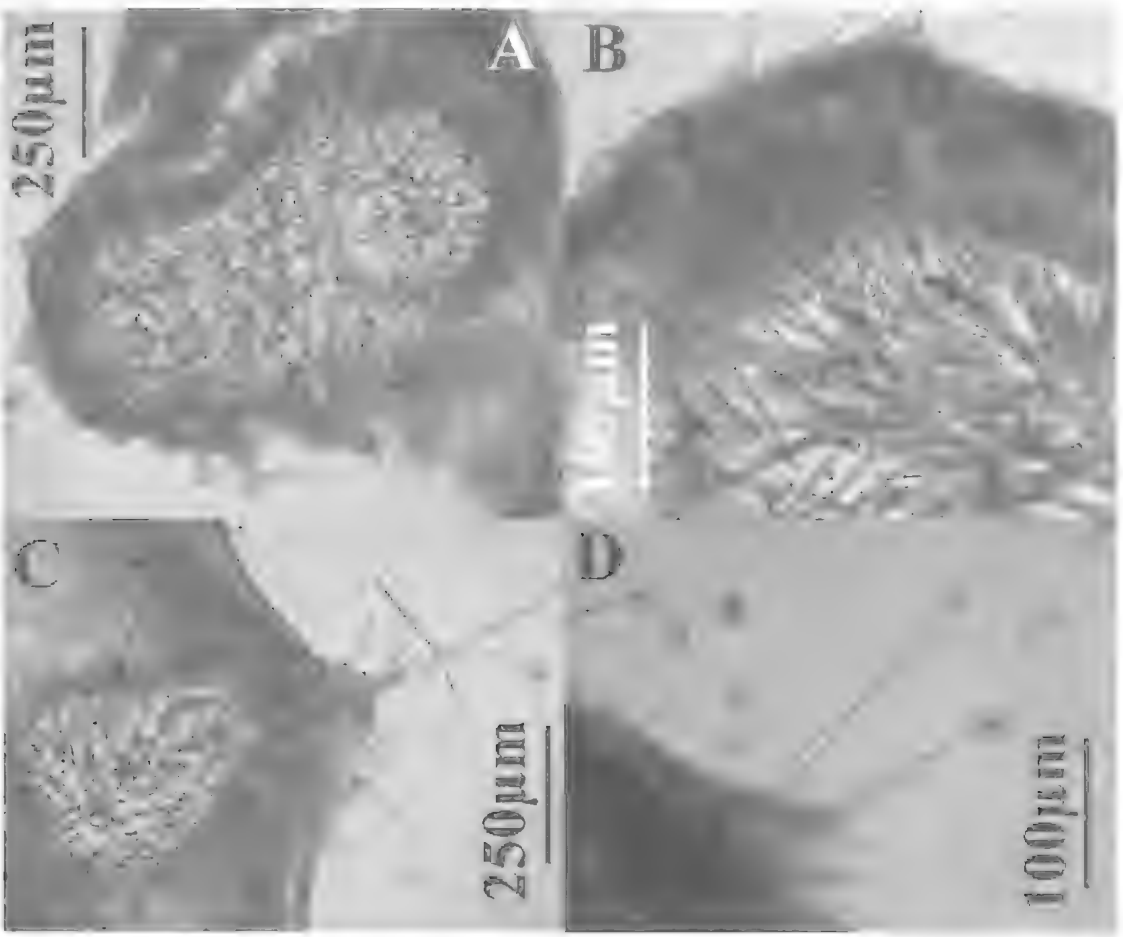



FIG. 16. *Aulospongus samariensis* sp. nov. (E Caribbean population, paratype QMG313310) A, Choanosomal skeleton. B, Peripheral skeleton. C, Subectosomal extra-axial spicule and ectosomal skeleton. D, Ectosomal skeletal bundle.

diameter, generally smaller in the axis than periphery of the skeleton.

*Megascleres.* Larger choanosomal principal rhabdostyles long, thick; shaft is nearly straight; bases slightly rhabdose; bases also lightly subtylote to prominently tylote, with tyles terminal or subterminal; spination on spicules varies between E & W Caribbean populations (the former with more-or-less even spination although generally heavier at distal and apical ends than at centre, spines relatively large, recurved, hook-like; the latter with bases lightly spined or occasionally completely smooth, with small recurved spines concentrated on apical end of spicule, aspinose below basal swelling); points are tapering, fusiform (218-(322.2)-412× 9-(13.2)-18µm). Smaller echinating rhabdostyles short, relatively thick; shaft straight or slightly curved at centre; basal rhabd slight or occasionally completely straight; points fusiform tapering; bases range from slightly subtylote to well developed tylote; spines more evenly dispersed over whole spicule (as compared to the larger size class), sometimes less spinose below basal swelling than elsewhere, sometimes completely smooth below basal swelling; spines small, recurved (112-(181.2)-232×6-(9.3) -13µm). Several intermediate-sized rhabdostyles present, linking larger and smaller classes. Subectosomal extra-axial styles very long, thin; shaft straight or slightly curved near basal end, occasionally flexuous; base smooth, rounded or slightly subtylote; points tapering to long fusiform (920-(1814.5)-2750×8-(18.3)-26µm). Ectosomal auxiliary anisoxeas moderately long, thin; shaft slightly curved at centre, occasionally

TABLE 2. Comparison between spicule dimensions of eastern (Jamaican) and western (Colombian) populations of *A. samariensis* sp. nov.

| Spicule | E Caribbean | W Carribean |
|---|---|---|
| Choanosomal principal rhabdostyles | (218-(261.6)-355×10-(13.2)-18μm) | (310-(377.5)-412×9-(13.1)-16μm) |
| Echinating rhabdostyles | (112-(187.3)-210×6-(7.5)-11μm) | (145-(201.3)-232×8-(10.4)-13μm) |
| Subectosomal extra-axial styles | (920-(1144.6)->2500×8-(15.5)-25μm) | (1325-(2247.6)-2750×16-(19.7)-26μm) |
| Ectosomal auxiliary anisoxeas | (225-(584.4)-775×2.5-(4.2)-5.5μm) | (340-(515.3)-612×3-(4.1)-5.5μm) |

flexuous, sinuous or raphidiform; ends are asymmetrical with long tapering points and tapering rounded hastate base (225-(508.5)-775 ×2.5-(4.1)-5.5μm)

*Microscleres.* Absent.

ECOLOGY. *Aulospongus samariensis* has not been recorded from any other locality in the Colombian Caribbean. One of us (SZ) has extensively investigated rocky-reef complex areas down to a depth of 40m from the border of Panamá to Santa Marta in the continental coast of Colombia, and in the islands, atolls and banks of the San Andrés and Providencia Archipelago (San Andrés island, Old Providence island, Courtown Cays, Albuquerque Cays, Serrana Bank, Roncador Bank, Quitasueño Bank), SW Caribbean. The fact that this species has been found elsewhere only in deep, insular drop-offs (i.e. Jamaica), suggests it may be a deep water species, that comes up to shallower reefs (above 18m depth) at Santa Marta, where there is a seasonal upwelling of the colder water mass (called 'Subtropical Underwater', 19-25°C, usually localized between 100-200m depth in the Caribbean; Bula-Meyer, 1985). There are unpublished examples of other sponges (and many published records of algae), that follow this pattern, but this is the first published record of this phenomenon for sponges.

REMARKS. Initially the E (Jamaican) and W (Colombian) Caribbean populations were thought to be distinct species, showing some consistent differences in growth form (more elongate versus more bushy), ectosomal auxiliary spicule geometry (anisoxeas with fusiform points versus those with hastate points), ectosomal specialisation (ectosomal auxiliary spicule brushes concentrated mainly around surface conules versus evenly hispid surface), and skeletal structure (axial skeleton more compressed versus more reticulate, respectively). Spicule dimensions also varied slightly between the two populations (Table 2). However, upon further consideration these differences are less obvious than their similarities, particularly in spicule geometry, and the two populations are considered to be conspecific.

This species belongs to *Aulospongus* in having characteristic fused fibre-bundles forming a denser core in the axial part of the skeleton, and a predominantly plumose structure towards the periphery; lacking any prominent differentiation between axial and extra-axial skeletons apart from the amalgamation of these fibres towards the centre of the skeleton, and having fibres which are cored and echinated by heavy bundles of rhabdostyles, in two size classes.

*Aulospongus samariensis* differs from the 'typical tubular' *Aulospongus* in its growth form (cylindrical club-shaped), rhabdostyle morphology (more-or-less even spination on both size classes of spicules, slightly less spined in the basal end, and with only a slight basal rhabd), possession of very long subectosomal extra-axial spicules protruding through the surface (in this regard similar only to *A. involutum* (Kirkpatrick)), and possession of a more-or-less well developed, specialised raspailiid ectosomal skeleton. Ectosomal skeletons are well developed in only two species of *Aulospongus* (*A. gardineri* and the present species), consisting of plumose brushes of ectosomal auxiliary styles/anisoxeas surrounding longer subectosomal extra-axial styles/anisoxeas. By comparison, vestigial ectosomal skeletons are present in three species (*A. involutum*, *A. novaecaledoniensis* sp. nov., *A. tubulatus*), consisting of ectosomal auxiliary styles/anisoxeas scattered on or below the surface, but not forming brushes and not necessarily associated with protruding subectosomal extra-axial styles/anisoxeas. Ectosomal auxiliary spicules and a specialised 'raspailiid' ectosomal structure are absent in four species (*A. cerebella*, *A. monticularis*, *A. spinosum*, and *A. villosa*), presumably a derived condition.

This species is similar to *A. gardineri* in ectosomal skeletal structure, *A. involutum* in possession of long subectosomal extra-axial spicules, and to both these species plus *A. novaecaledoniensis* in having both categories of rhabdostyles partially spined. In other details,

however, it differs substantially from all other species, particularly in spicule geometries (Table 1) and dimensions (Table 2).

To some extent this species also resembles *Raspailia acanthifera* (George & Wilson, 1919: 159) from North Carolina, particularly in its growth form (lobate, with lamellate branches), some aspects of skeletal architecture (longitudinal multispicular fibres at the core of the skeleton with only few interconnecting paucispicular transverse fibres; peripheral fibres becoming more radial with fewer interconnecting tracts towards the surface; peripheral fibres fully cored by styles which eventually project through surface in bundles forming surface conules), and ectosomal characteristics (projecting long subectosomal extra-axial styles forming loose bundles at the surface). Conversely, spicule morphology and spicule distribution within the skeleton differ substantially between the two species. In *R. acanthifera* there are five categories of megascleres, each substantially different from those of *A. samariensis* sp. nov., and skeletal structure of *R. acanthifera* is also markedly axially compressed, indicating the latter species should be assigned to *Raspailia* (*Raspaxilla*) (see below), whereas this species is more appropriately referred to *Aulospongus*.

Colombian populations of *A. samariensis* were found to contain both slight antimicrobial against *Staphylococcus aureus* (for ethanol and chloroform extracts) (Silvestri, Zea & Duque, 1994), and strong antitumor activity (Zea, unpublished data), further supporting the relatively high incidence of 'biological activity' reported amongst species of Raspailiidae (Hooper et al., 1992).

**Aulospongus spinosum** (Topsent, 1927)
(Fig. 17, Table 1)

*Rhaphidectyon spinosum* Topsent, 1927: 15; 1928: 288, pl. 2, fig. 5, pl. 9, fig. 28, pl. 10, figs 2-3; Lévi, 1960: 752, fig. 7.

*Aulospongus spinosum*; Hooper, 1991: 1307, fig. 65g-i; Maldonado, 1992: 1149-1150, fig. 9e-j.

MATERIAL. HOLOTYPE. MOM (schizotypes MNHN LBIM DT1139, BMNH1930.7.1.39): Cape Verde Is, near São Vicente I., 16 48'N, 25 06'W, coll. 'Princesse-Alice', 29.vii.1901, 219m depth.

DISTRIBUTION. São Vicente I., North Atlantic, Alboran I., Mediterranean.

DESCRIPTION. Growth form bulbous, erect. Surface shaggy, conulose. Colour dark grey in ethanol. 'Raspailiid ectosomal skeleton' absent, with only larger smooth rhabdostyles protruding through the surface forming shaggy surface processes. Choanosomal skeleton distinctly plumose in both axial and extra-axial regions, composed of very stout, widely separated ascending fibre-bundles with very few interconnecting tracts. Fibres cored by larger (smooth) styles and rhabdostyles (virtually inseparable in their morphology), forming radial tracts in the axis of the skeleton but becoming progressively thicker towards the periphery, ending in discrete plumose bundles at the surface. Largest rhabdostyles/styles appear to be located in the peripheral skeleton. Megascleres include long, thick, choanosomal principal styles and rhabdostyles, completely smooth, with very slight to moderate basal rhabd, the largest occasionally nearly straight at the base (770-1085×28-43μm). Two sizes of smaller rhabdostyles present: long, slender ones, completely smooth, with well curved basal rhabd, predominantly found in choanosomal and peripheral fibres, protruding from fibres at slightly acute angles (90-185×5-12μm), and true echinating acanthostyles with only slight or no basal rhabd, relatively evenly spined, *Eurypon*-like, with swollen subtylote bases bearing very large perpendicular spines (75-145×7-10μm). Subectosomal extra-axial and ectosomal auxiliary spicules absent. Microscleres are raphides occurring singly or in trichodragmata (40-50μm long).

REMARKS. The second category of (smooth) echinating rhabdostyles was overlooked by previous authors, and appears to be quite different from the acanthose echinating acanthostyles. In this regard it is similar to *A. gardineri*, although differing in most other characters (e.g. spicule morphology and spination, spicule sizes, growth form, lack of specialised ectosomal skeleton and possession of raphides in *A. spinosum*).

This species is also highly derived, reduced in most of its morphological characters, and differs from other known *Aulospongus* in having raphide microscleres dispersed throughout the skeleton. Although several other species of *Aulospongus* have been described at some time or another with raphide microscleres, re-examination of relevant type and other material has confirmed that in all cases these were vestigial (raphidiform) ectosomal auxiliary spicules, whereas in *A. spinosum* these appear to be genuine raphides/ trichodragmata.

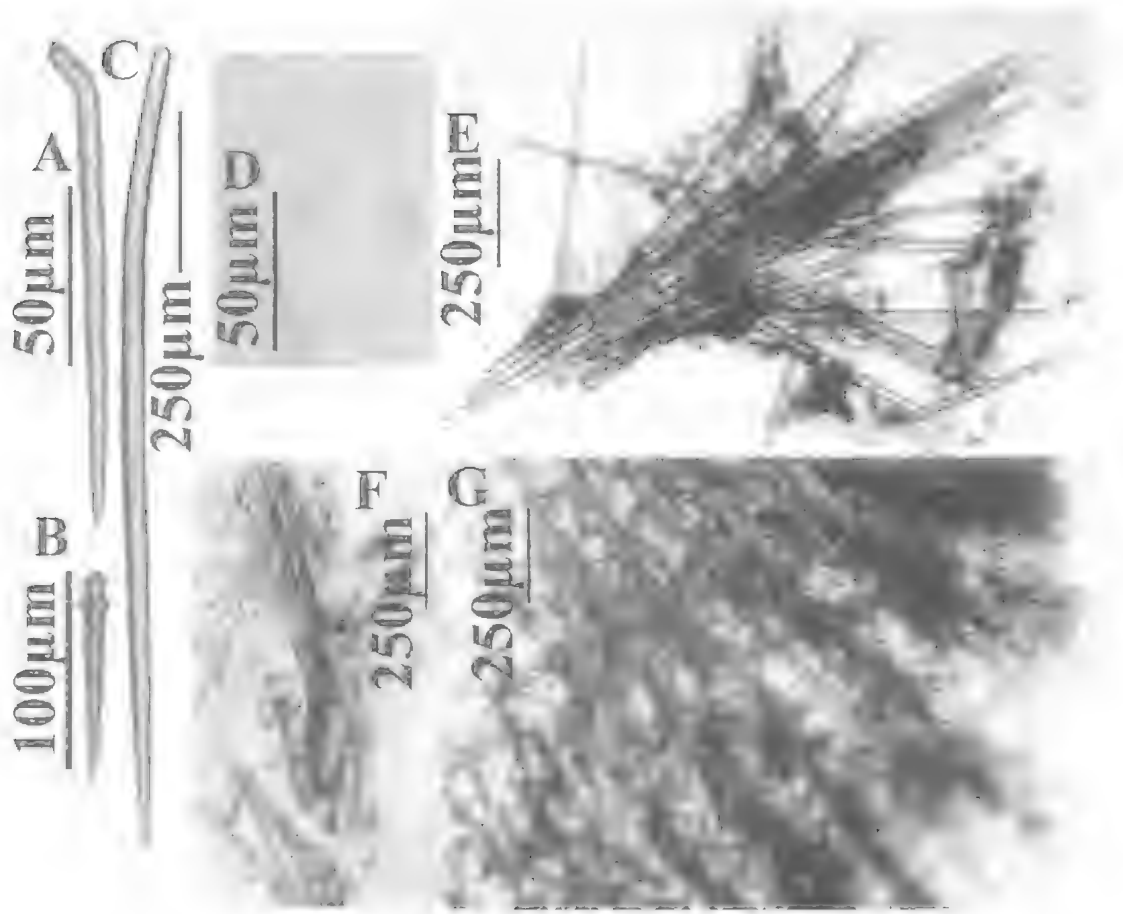



FIG. 17. *Aulospongus spinosum*. A, Third category of rhabdostyle. B, Echinating style/rhabdostyle. C, Choanosomal principal rhabdostyle. D, Raphides. E, Ectosomal auxiliary spicule bundle. F, Choanosomal fibre bundle. G, Choanosomal skeleton.

Nevertheless, Maldonado (1992) notes that raphides appear to be associated with, and possibly reinforce, the pinacoderm. If this correct, it is possible that these raphides may be extremely vestigial ectosomal auxiliary megascleres rather than typical microscleres. Unfortunately no well-fixed material is available to undertake more comprehensive histological analysis to explore this possibility, and for the moment these spicules are assumed to be microscleres.

**Aulospongus villosa** (Thiele, 1898)
(Figs 18-19, Table 1)

*Raspailia* (?) *villosa* Thiele, 1898: 60, pl. 4, fig. 10, pl. 8, fig. 48; Koltun, 1970: 270, fig. 32, pl. 8, fig. 4; Hoshino, 1987: 19; Tanita & Hoshino, 1990: 102; Sim, 1990: 317.
*Heterectya villosa*; Hallmann, 1917: 393; [? doubtful record of Burton, 1959: 45].
*Aulospongus villosa*; Hooper, 1991: 1307, fig. 65d-f.

MATERIAL. HOLOTYPE. ZMB2204: Hakodate, Japan, coll. Hilgendorf.

DISTRIBUTION. Japan (Hakodate, Sagami Bay), Korea (Japan Sea & Jeju I.) and Russia (Iturup I., Kurile Is, Sea of Ochotsk). Burton's (1959) record from Iceland is dubious. He did not provide a description of the specimen, no voucher material was cited, and it is therefore ignored here.

DESCRIPTION. Growth form massive, subspherical, bushy. Surface prominently shaggy, conulose. Colour light brown in ethanol. 'Raspailiid ectosomal skeleton' absent, with only tufts of choanosomal principal rhabdostyles protruding. Choanosomal skeleton exclusively plumose, composed of relatively thick, compressed fibre-bundles in which the larger rhabdostyles are confined completely within

ascending fibres. Smaller rhabdostyles exclusively echinate fibres, standing nearly perpendicular to them, often touching those on adjacent, opposing fibres, together producing the superficial impression of a lattice-like, reticulate skeleton. No notable compression of the axial skeleton, and no specialised subectosomal extra-axial megascleres present. Megascleres consist of larger choanosomal principal rhabdostyles with moderate to strongly developed basal rhabd, usually completely smooth or with small granular spines scattered over the apical half (235-370×10-16µm). Smaller echinating rhabdostyles vary from completely smooth to partially spined on the apical half, usually with a very strong basal rhabd but occasionally straight, spines very small, granular (142-165×4-10µm). Subectosomal extra-axial and ectosomal auxiliary spicules absent. Microscleres absent.

REMARKS. This is a very reduced species of *Aulospongus*, similar to *A. cerebella*, *A. flabellum* and *A. spinosum*, lacking any ectosomal auxiliary or subectosomal extra-axial spicules, and having only two categories of rhabdostyles. Rhabdostyles in *A. villosa* resemble to some extent those of *A. involutum*, *A. gardineri* and *A. novaecaledoniensis* sp.nov, in geometry and approximate size, but whereas those of *A. villosa* are often completely smooth or have small granular spines the other three species have very large, recurved spines covering only the apex of rhabdostyles.

## REVIEW OF OTHER RASPAILIIDAE WITH RHABDOSTYLES

### **Raspailia** Nardo, 1833
### Subgenus **Raspaxilla** Topsent, 1913

*Raspaxilla* Topsent, 1913: 616; Bergquist, 1970: 28; Hooper, 1991: 1195, 1245. Type species: *Raspaxilla phakellina* Topsent, 1913: 617, by monotypy.

*Echinaxia* Hallmann, 1916a: 543; 1917: 391; de Laubenfels, 1936: 102; Bergquist, 1970: 30; Hooper, 1991: 1195. Type species: *Axinella frondula* Whitelegge, 1907: 509, by original designation.

*Axinectya* Hallmann, 1917: 393; Hooper, 1991: 1195. Type species: *Axinella marlana* Ridley & Dendy, 1886: 480, by original designation.

DEFINITION. *Raspailia* with echinating acanthose rhabdostyles. Larger choanosomal principal styles completely smooth, without any basal rhabd, geometrically distinct from smaller acanthose echinating rhabdostyles. Axial skeleton well differentiated from extra-axial skeleton: axial skeletal compressed, composed of reticulate tracts cored by choanosomal principal styles; extra-axial skeleton plumo-reticulate, with plumose ascending tracts interconnected by transverse tracts both cored by choanosomal principal styles (forming a reticulation), or reduced to radial tracts of single long subectosomal extra-axial styles embedded in and perpendicular to axis, protruding through the surface. Echinating rhabdostyles generally more abundant in peripheral skeleton than in axis.

REMARKS. Seventeen species are currently assigned to *Raspailia* (*Raspaxilla*), including species transferred here from *Endectyon*, *Hemectyon* and *Aulospongus*. *Raspaxilla* has a wide geographic distribution, ranging from the Indo-west Pacific (N and S New Zealand, NW Australia, N Great Barrier Reef, central NSW, New Caledonia, Japan, Micronesia), E coast of the United States of America (North Carolina), central E Pacific and the antarctic-subantarctic region (Fig. 35). Apart from the Southern (subantarctic) Ocean, *Raspaxilla* has not yet been recorded in either the Atlantic or the E or central Indian Oceans, and is assumed (from present data) to be a Pacific rim species (Fig. 35). It is possible that the specimen described by Pulitzer-Finali (1994) as '*Endectyon humanum*' from Kenya belongs to *Raspaxilla*, but this species is barely recognisable from his description and for the moment is *incertae sedis*.

Essentially *Raspailia* (*Raspaxilla*) differs from *Aulospongus* in having echinating rhabdostyles geometrically very different from the usually longer choanosomal principal styles (the latter without any basal rhabd); the subectosomal extra-axial styles form a radial skeleton perpendicular to the axis; and axial and extra-axial skeletons are well differentiated (the former compressed, the latter plumoreticulate and/or radial). Placement of all species, however, is not always straightforward given that some taxa may lose certain characters (e.g. extra-axial skeleton becomes reduced to single long subectosomal extra-axial spicules embedded in the axis and forming a radial skeleton; or the subectosomal extra-axial spicules are lost completely). There is also a correlation between the localisation of echinating rhabdostyles in the peripheral skeleton and the degree of axial compression. In species with very compressed skeletons the extra-axial skeleton is reduced to single long subectosomal extra-axial spicules (without reticulate connections) and the

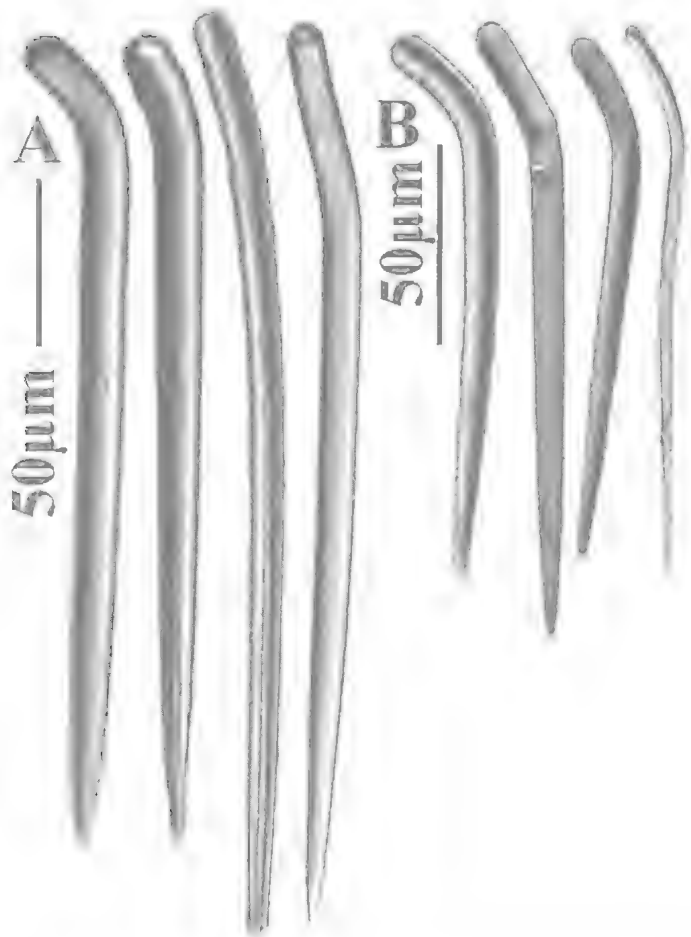



FIG. 18. *Aulospongus villosa.* A, Choanosomal principal rhabdostyles. B, Echinating rhabdostyles.

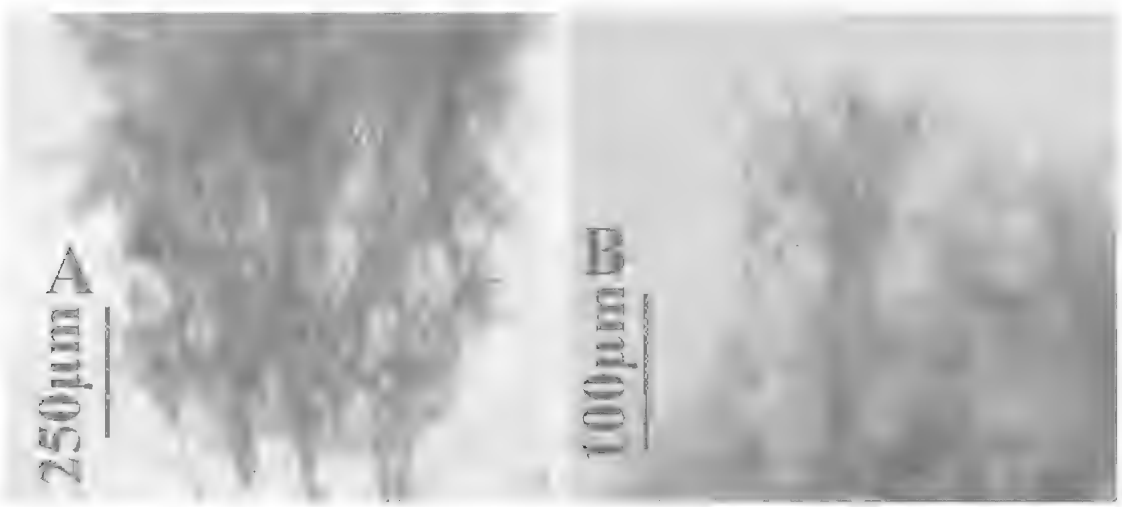



FIG. 19. *Aulospongus villosa.* A, Choanosomal skeleton. B, Peripheral skeleton.

echinating rhabdostyles are literally 'pushed' into the ectosomal skeleton where they form brushes or produce a continuous palisade.

### Raspailia (Raspaxilla) phakellina
(Topsent, 1913)
(Fig. 20, Table 1)

*Raspaxilla phakellina* Topsent, 1913: 617, pl. 1, fig. 4, pl. 6, fig. 15; Burton, 1932: 326; Boury-Esnault & van Beveren, 1982: 51, pl. 7, fig. 26, fig. 12.
*Raspailia (Raspaxilla) phakellina*; Hooper, 1991: 1196, fig. 7k-l.

MATERIAL. HOLOTYPE. MOM (fragment MNHN LBIM DT1614): Burwood Bank, Antarctica, 54°25'S, 57°32'E, 112m depth, 1.xii.1903. OTHER MATERIAL. BMNH1928.2.15.781a, 846a: Falkland Islands, Argentina, RRS 'Discovery', 75-82m depth.

DISTRIBUTION. Antarctic - subantarctic region (Antarctica, Falkland Is, Kerguelen Is).

DESCRIPTION. Erect, digitate, arborescent, with enlarged basal holdfast attachment and branching in one plane. Surface slightly conulose, hispid. Colour whitish cream to yellowish in ethanol. 'Raspailiid ectosomal skeleton' present but not well developed, consisting of long subectosomal extra-axial styles protruding through the surface, surrounded at their bases by wispy bundles of ectosomal auxiliary anisoxeas forming stellate bundles nearly parallel to the surface. Choanosomal skeleton with well differentiated axial and extra-axial regions. Axial skeleton compressed, strongly reticulate, composed of multispicular fibres cored by choanosomal principal styles and echinated sparsely by echinating rhabdostyles. Extra-axial skeleton plumo-reticulate, with ascending multispicular fibres cored by choanosomal principal styles and profusely echinated by rhabdostyles, diverging towards the periphery, interconnected by transverse pauci- or multispicular fibres which persist all the way to the surface. Echinating rhabdostyles predominant in extra-axial skeleton. Megascleres include long choanosomal principal styles, slightly curved centrally or straight, with evenly rounded, smooth, non-rhabdose bases (550-900× 10-16μm). Echinating rhabdostyles moderately long, with slightly rhabdose and subtylote bases, completely smooth or with small, erect spines confined to apical two-thirds of spicule (140-370×8-18μm). Subectosomal extra-axial styles long, thick, straight or slightly curved, entirely smooth (1100-1450×12-18μm). Ectosomal auxiliary styles wispy, raphidiform, straight, centrally curved or sinuous (450-650× 2-3μm). Microscleres absent.

REMARKS. Comparisons between the holotype (Antarctica) and Kerguelen specimens, with the 'Discovery' material described by Burton (1932) show some differences: notably the complete lack of spines on rhabdostyles in the latter specimen (whereas some rhabdostyles have apical spines in the former specimens), and the persistence of the plumo-reticulate extra-axial skeleton for most of the sponge diameter, with only a relatively small, confused, slightly compressed axial component (as compared to a relatively larger central axial skeleton in the holotype and Kerguelen specimen). Nevertheless, there is no doubt that all three specimens belong to the same species. *Raspailia (Raspaxilla) phakellina* differs substantially from other *Raspailia* species only in having basal rhabds on echinating acanthostyles, and having its extra-axial skeleton dominated by ascending fibres reminiscent of *Aulospongus*, but in which transverse connecting fibres persist all the way to the surface and produce a plumo-reticulate skeletal structure (rather than a purely plumose skeleton characteristic of *Aulospongus*).

### Raspailia (Raspaxilla) acanthifera
George & Wilson, 1919

*Raspailia acanthifera* George & Wilson, 1919: 159, pl. 62, fig. 34, pl. 63, fig. 38-39, pl. 66, fig. 59.

MATERIAL. HOLOTYPE. USNM (not seen): Fort Macon beach, Beaufort, North Carolina.

DISTRIBUTION. E coast of USA (North Carolina).

DESCRIPTION.Growth form stalked, lobate, with lamellate branches. Surface with hispid ridges but smooth between ridges. Colour grey-brown with tinge of yellow in ethanol. 'Raspailiid ectosomal skeleton' well developed with projecting long subectosomal extra-axial styles surrounded by ectosomal auxiliary anisoxeas forming loose bundles at the surface. Skeletal architecture with well differentiated axial and extra-axial components. Axial skeleton compressed, with mainly thicker longitudinal fibres fully cored with spicules, loosely interconnected by few transverse paucispicular fibres, together producing a loose, open reticulation. Extra-axial skeleton radial, with fewer interconnecting tracts towards the periphery, but persisting all the way to the surface, and with tracts fully cored by styles.

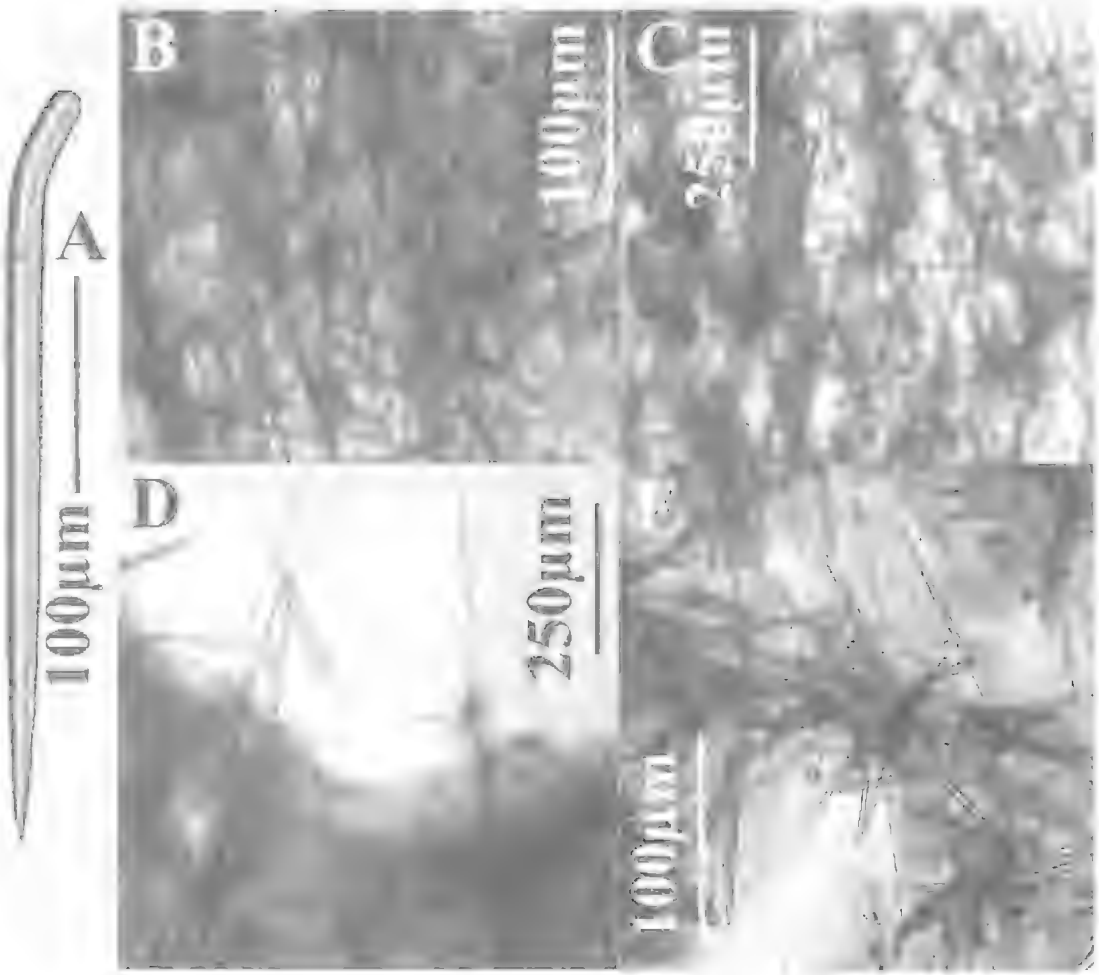



FIG. 20. *Raspailia (Raspaxilla) phakellina*. A, Echinating rhabdostyle. B, Reticulate axial skeleton. C, Plumo-reticulate extra-axial skeleton. D, Ectosomal skeleton. E, Reticulate axial fibres.

Fibres more bulbous near the surface than in the axial region, and subectosomal extra-axial styles embedded in peripheral fibres project through surface in bundles forming surface conules. Echinating rhabdostyles predominant in the peripheral skeleton, participating in 'raspailiid ectosomal spicule brushes', as well as echinating radial (connecting) fibres near the surface. Five categories of megascleres present. (1) Short, curved, entirely smooth choanosomal principal styles (160-260×7-12µm), coring most fibres and producing the spicule bundles at the surface. (2) Straight, thick styles (160-240×12-20µm) intermingled with the shorter styles in both the peripheral and deeper parts of the skeleton, presumably modifications to choanosomal principal spicules. (3) Echinating acanthose rhabdostyles (80-120×6µm), with strongly recurved spines over most of the spicule although spines are characteristically absent from the slightly subtylote base, and the base slightly rhabdose. (4) Long, slender subectosomal extra-axial styles (400-600×6-7µm), protruding through the surface. (5) Slender, raphidiform, ectosomal auxiliary anisoxeas (200×1µm) dispersed mainly within the ectosomal skeleton, singly or in loose bundles (described as raphides). Microscleres absent (George & Wilson, 1919).

REMARKS. Skeletal structure of *R. acanthifera* is characteristically axially compressed, with well differentiated axial and extra-axial skeletons, well developed ectosomal skeleton, and geometrically different echinating rhabdostyles and choanosomal principal styles, indicating that it is most appropriately assigned

to *Raspailia* (*Raspaxilla*) and not to *Aulospongus*.

**Raspailia (Raspaxilla) clathrioides**
(Lévi, 1967)
(Figs 21, 36C)

*Aulospongus clathrioides* Lévi, 1967: 21, text-fig. 5, pl. 2, fig. c; Hooper, 1991: 1311, fig. 67a-d; Hooper & Lévi, 1993: 1295, figs 40-41; Hooper & Battershill, 1998: 136.

MATERIAL. HOLOTYPE. MNHN LBIM DCL823: Canala, Melasceu, New Caledonia, coll. 'Singer-Polignac', 4.i.1962, 22°30'S, 166°45'E, 35m depth. OTHER MATERIAL. New Caledonia (refer to Hooper & Lévi, 1993).

DISTRIBUTION. Known only from the SW New Caledonian lagoon.

DESCRIPTION. Growth form stalked, arborescent, bushy, cylindrical-branching. Surface shaggy, prominently conulose. Colour yellow-orange alive. 'Raspailiid ectosomal skeleton' either completely absent or with very few vestigial ectosomal auxiliary styles/anisoxeas, forming vestigial brushes surrounding protruding choanosomal principal styles or scattered below the surface. Subectosomal extra-axial spicules absent. Surface dominated by swollen fibres and plumose brushes of smooth styles both producing surface conules. Choanosomal skeleton predominantly plumose or plumo-reticulate, with a slightly compressed reticulate axial core dominated by well developed spongin fibres, with the spicule skeleton proportionally reduced. Axial fibres are vestigially cored by choanosomal principal styles. Extra-axial fibres are prominently plumose and heavily multispicular, with fewer paucispicular interconnecting fibres persisting in the peripheral skeleton and to the surface. Echinating rhabdostyles are slightly more abundant in the peripheral skeleton than in the axis. Megascleres include choanosomal principal styles, smooth, slightly curved or occasionally sinuous, sometimes modified to anisoxeas, only occasionally with a very faint basal curvature (145-454×3-7μm). Echinating rhabdostyles, microcionid-like, long, slender, straight or slightly curved towards the basal end, with a relatively well developed basal swelling, straight base or only slight basal rhabd, evenly spined except for smooth base, spines small, granular (58-82×1.5-4μm). Subectosomal extra-axial spicules absent. Ectosomal auxiliary styles and anisoxeas present or absent, always very rare, raphidiform, straight or sinuous (97-134× 0.8-1.5μm). Microscleres absent.

REMARKS. This species is a borderline case between *Aulospongus* and *Raspaxilla*, and is referred here to *Raspailia* (*Raspaxilla*) given that the ascending fibre system has transverse connecting fibres extending all the way from the axis to the surface (producing a plumo-reticulate rather than a strictly plumose skeleton as is typical for *Aulospongus*); the axial and extra-axial skeletons are slightly differentiated (reticulate versus plumo-reticulate), with the axis showing slight compression; the larger choanosomal principal styles are entirely smooth, and they have no, or at most only very faint, basal curvature (i.e. only a few might be termed vaguely rhabdose), and furthermore, anisoxeote modifications of choanosomal principal spicules are relatively common, indicating that choanosomal principal and echinating spicules are morphologically quite distinct; and the smaller echinating rhabdostyles also have only slight basal rhabds, more in common with species of *Raspaxilla* than with *Aulospongus*.

This is a sister species of *R.* (*Raspaxilla*) *reticulata* (N Great Barrier Reef) and *R.* (*R.*) *topsenti* (N New Zealand), having a similar arborescent growth form, echinating rhabdostyles with swollen, smooth, straight- or relatively poorly rhabdose-bases (at least compared to most species of *Raspaxilla* and *Aulospongus*); the reticulate axial region is slightly compressed; and the extra-axial skeleton is plumo-reticulate in which the ascending plumose fibres dominate but the reticulate fibre connections persist all the way to the surface. The three species differ in their spicule compositions (presence of a specialised ectosomal skeleton in *R.* (*R.*) *reticulata*, including possession of long subectosomal extra-axial styles; vestigial ectosomal auxiliary styles/anisoxeas in *R.* (*R.*) *topsenti*), spicule sizes (compare with the respective descriptions below), morphology of choanosomal principal styles (particularly *R.* (*R.*) *topsenti*), and greater dominance of the reticulate versus plumose components of the skeleton in both the other species.

Re-examination of the material described as *Aulospongus clathrioides* by Hooper & Lévi (1993) also found that one specimen out of four contained very few vestigial ectosomal auxiliary styles/anisoxeas scattered below the surface, or occasionally forming sparse brushes surrounding

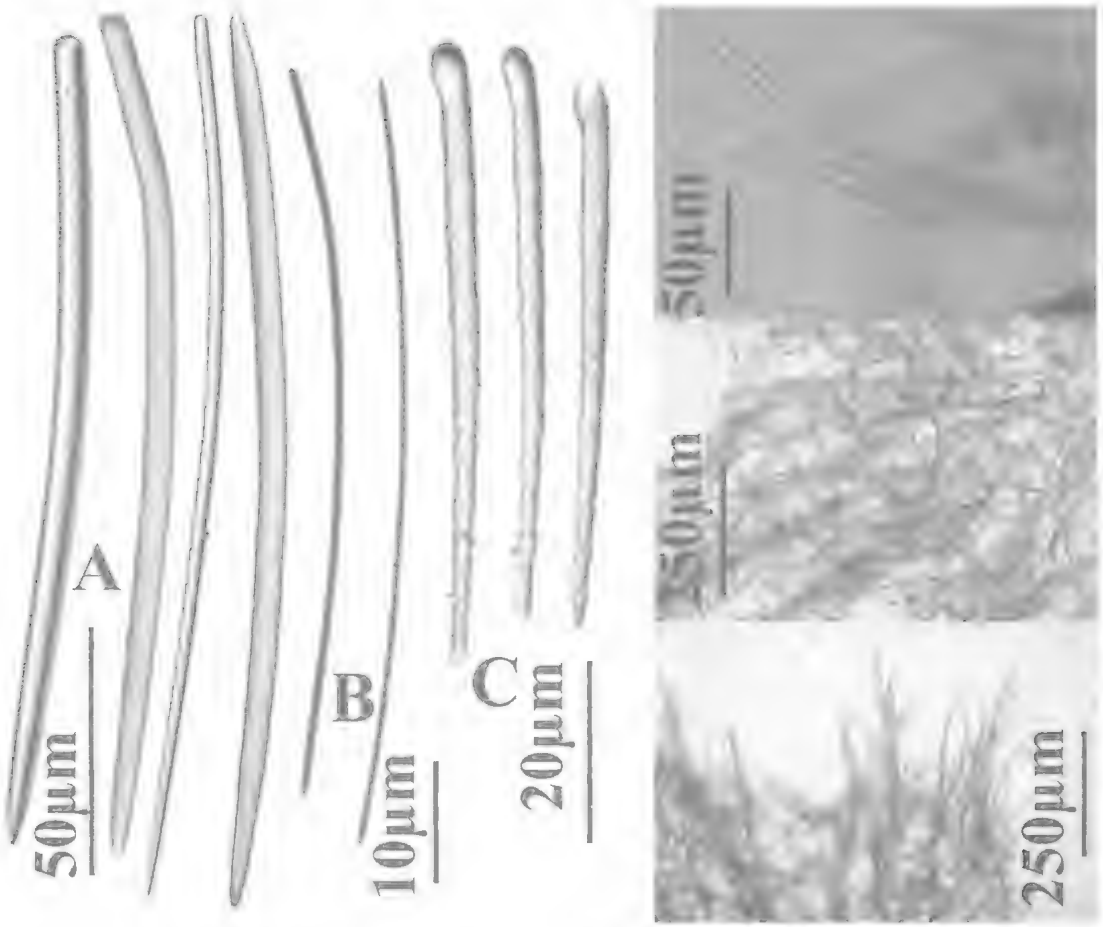



FIG. 21. *Raspailia (Raspaxilla) clathrioides.* A, Choanosomal principal styles/anisoxeas. B, Ectosomal auxiliary anisoxeas. C, Echinating rhabdostyles. D, Ectosomal skeleton. E, Reticulate axial skeleton. F, Plumo-reticulate extra-axial skeleton.

choanosomal principal styles in the peripheral skeleton. These are obviously the remnants of a specialised 'raspailiid ectosomal skeleton', but this feature is so vestigial and rare in the 5 described specimens of *R.* (*R.*) *clathrioides* (i.e. absent in the holotype), that it can hardly be constituted as a character 'typical' for the species. These vestigial ectosomal auxiliary spicules are also present in *R.* (*R.*) *topsenti*, and both species lack any subectosomal extra-axial spicules, whereas the ectosomal skeleton of *R.* (*R.*) *reticulata* is consistently well developed and 'typical' of Raspailiidae. Nevertheless, it is conceivable that all three species are geographic variants of a single species, with these observed differences being ones indicating isolated, intraspecific population variability rather than interspecific differences. Genetic comparisons are required to verify this supposition.

**Raspailia (Raspaxilla) compressa**
Bergquist, 1970
(Fig. 22)

*Raspailia compressa* Bergquist, 1970: 29-30, text-fig. 3a, pls 7b, 11a; Hooper, 1991: 1245, figs 32-33.

MATERIAL. HOLOTYPE. MONZ POR 30: NE. of North Cape, New Zealand, 173° 04'E, 34° 28'S, 54 m depth. OTHER MATERIAL. NTM Z1748: W of Port Hedland, Northwest Shelf, WA, 19° 05.1'S, 118° 47.7'E, 84m depth, coll. 'Soela'.

DISTRIBUTION. North Cape, New Zealand; Northwest Shelf, Western Australia.

DESCRIPTION. Growth form arborescent, stalked, digitate, with bifurcating, cylindrical or slightly flattened branches. Colour bright yellow in life. Surface hispid, otherwise even. 'Raspailiid ectosomal skeleton' present composed of plumose brushes of ectosomal auxiliary anisoxeas surrounding bases of subectosomal extra-axial styles (the latter protruding through the surface), and also with bundles of rhabdostyles intermingled with spicule brushes on the surface, both perched on ends of the peripheral extra-axial skeletal tracts. Axial and extra-axial skeletons well differentiated. Axial skeleton heavily compressed, consisting of a close-meshed reticulation of multispicular fibres cored by choanosomal principal styles mostly orientated along longitudinal axis of branches, interconnected by pauci- or multispicular transverse skeletal tracts. Extra-axial skeleton plumo-reticulate with multispicular ascending tracts interconnected by paucispicular transverse tracts. Ascending tracts in peripheral skeleton with long subectosomal extra-axial styles embedded and extending a long way through surface. Echinating rhabdostyles concentrated on fibres at the junction of axial and extra-axial skeletons, usually in thick bundles. Megascleres include choanosomal principal styles slightly curved towards basal end, with rounded non-tylote bases, without any basal rhabd (240-449×6-25μm). Echinating rhabdostyles with basal rhabd varying from prominent to slightly bulbous, nearly straight, and with smooth base and small granular spines on apical third of spicule (93-360×4-9μm). Long subectosomal extra-axial styles relatively thick, slightly curved near base or straight, with rounded or slightly subtylote bases (887-1400×16-24μm). Ectosomal auxiliary anisoxeas nearly rhaphidiform, flexuous, sometimes straight or slighlty curved at centre, occasionally stylote (234-360×2-4μm). Microsclere absent.

REMARKS. Bergquist (1970) suggested that this species had close affinities to *Aulospongus* based on rhabdostyle geometry, but skeletal structure (compressed axis, reticulate extra-axis), lack of any basal rhabds on choanosomal principal styles, and lack of plumose fibre-bundles indicate that it belongs to *Raspaxilla*. This species shows some similarities to *R.* (*Raspaxilla*) *clathrioides* and *R.* (*Raspaxilla*) *reticulata* (compare descriptions above and below). As mentioned by Hooper (1991), there is some doubt about the conspecificity of the New Zealand and Western Australian populations, given that they appear to differ only in the lengths of echinating acanthostyles (half as long in the Western Australian population), and slightly in their live colouration. No other observed features were able to differentiate the two populations based on existing material.

**Raspailia (Raspaxilla) flaccida**
Bergquist, 1970

*Raspailia flaccida* Bergquist, 1970: 27: pls 6b, 10b, 18c.
*Raspailia* (*Raspaxilla*) *flaccida*; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE. MONZ POR29 (not seen): Menzies Bay, Christchurch, New Zealand

DISTRIBUTION. Known only from S New Zealand.

DESCRIPTION. Growth form digitate, irregularly branching, thickly cylindrical digits. Surface conulose, hispid. Colour bright orange in life. 'Raspailiid ectosomal skeleton' vestigial, consisting of rhaphidiform styles/anisoxeas lying in poorly defined groups at the surface. Axial and extra-axial skeletons well differentiated. Axial skeleton plumo-reticulate, with fibres cored by choanosomal principal styles/oxeas. Extra-axial skeleton with ascending fibres, more slender than axial fibres, cored by paucispicular tracts of mainly choanosomal principal styles (fewer oxeas), branching towards the surface, interconnected by sparse unispicular tracts. Echinating rhabdostyles predominant in extra-axial skeleton. Megascleres consist only of choanosomal principal styles/oxeas of a single size category but with very variable terminations, also varying in curvature from straight to contorted, and points often mucronate (314-790×9-14μm). Echinating rhabdostyles with smooth, slight basal rhabd, small granular spines covering apical 2/3 of spicule, occasionally modified to acanthoxeas with central bend (121-145×5-7μm). No special category of subectosomal extra-axial spicules. Ectosomal auxiliary styles/anisoxeas vestigial, rhaphidiform, slightly curved or toxiform (up to 340×1.5μm). Microscleres absent (Bergquist, 1970).

REMARKS. This species is unlike all other described *Raspaxilla*, being substantially reduced in many of its characters, notably: vestigial ectosomal specialisation, lacking any subectosomal extra-axial spicules, reduced reticulate connections between ascending extra-axial tracts, and many geometric modifications to megascleres. Nevertheless, the possession of axial and extra-axial

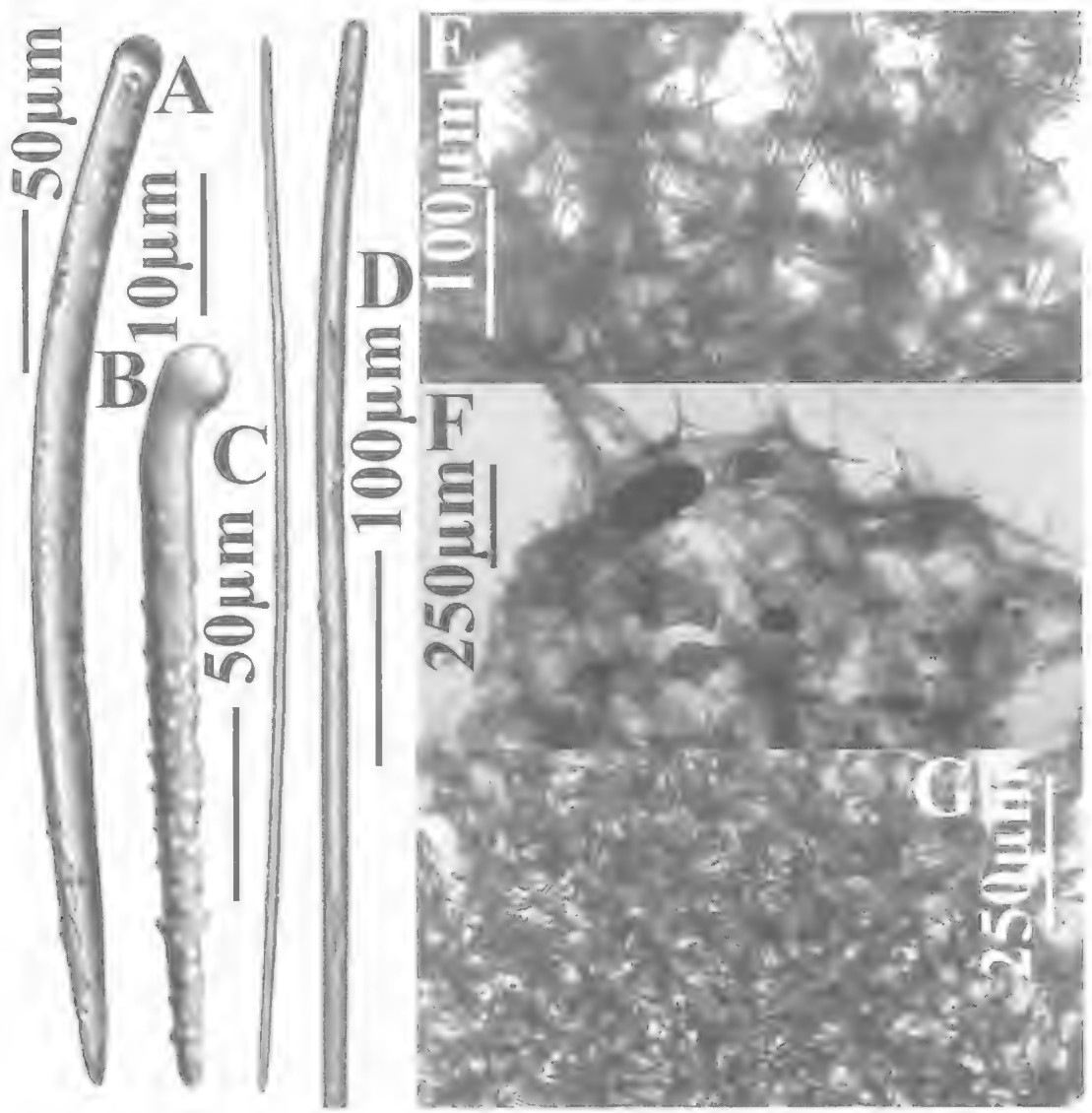



FIG. 22. *Raspailia (Raspaxilla) compressa.* A, Choanosomal principal subtylostyle. B, Echinating rhabdostyle. C, Ectosomal auxiliary anisoxea. D, Basal end of subectosomal extra-axial style. E, Plumo-reticulate fibres in extra-axial skeleton. F, Ectosomal skeleton and detritus incorporated into skeleton. G, Reticulate axial skeleton.

differentiation, axial compression, non-rhabdose choanosomal principal megascleres together with echinating rhabdostyles indicate that it is most appropriately included in *Raspaxilla*.

### **Raspailia (Raspaxilla) folium** Thiele, 1898

*Raspailia folium* Thiele, 1898: 60, pl. 3, fig. 7, pl. 8, fig. 47a-c; Hoshino, 1976: 6, pl. 1, figs 6-7; Hoshino, 1981: 215-216, fig. 7; Hoshino, 1987: 18; Tanita & Hoshino, 1990: 99, pl. 10, fig. 8, text-fig. 61; Sim, 1990: 317.
*Echinaxia folium*; Hallmann, 1917: 392.
*Raspailia* (*Raspaxilla*) *folium*; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE. ZMB (not seen): Enoshima, Japan.

DISTRIBUTION. Japan (Enoshima, Sagami Bay, Ariake Sea) and Korea (Sea of Japan, Jeju I., South Sea).

DESCRIPTION. Growth form stalked, flabellate, vasiform, with thin lamellae. Surface rough, minutely hispid. Colour pinkish-brown alive. 'Raspailiid ectosomal skeleton' nearly vestigial, with raphide-like anisoxeas tangential to surface in sparse bundles or lying singly on

surface. Axial and extra-axial skeletons well differentiated. Axial skeleton reticulate, with fibres cored by small choanosomal principal styles. Extra-axial skeleton radial, with long tracts of choanosomal principal styles heavily echinated by rhabdostyles, and larger subectosomal extra-axial styles embedded in peripheral fibres and projecting a long way through the surface. Megascleres consist of entirely smooth, slender choanosomal principal styles, straight, slightly centrally curved or sinuous, evenly rounded or anisoxeote bases, without any basal rhabd (240-(292)-325× 5-(6.7)-11μm). Echinating rhabdostyles relatively large, thick, with basal rhabd varying from slightly curved to basal curvature nearly at right angles to the shaft, with smooth base and small spines restricted to the apical extremity or the apical 1/3 of spicule (141-(264)-500× 8-(12.5)-25μm). Subectosomal extra-axial styles thick, long, slightly curved near basal end, evenly rounded base and hastate point (up to 1120-(1236)-2000×16-(25)-36μm). Ectosomal auxiliary spicules raphidiform oxeotes or anisoxeas (asymmetrical ends), usually bent or sinuous (270-320×1.5-3μm). Microscleres absent (Thiele, 1898; Hoshino, 1981; Sim, 1990).

REMARKS. A search for the holotype, undertaken by the author and Dr D. Kühlmann at the ZMB in 1988, was unsuccessful. This species is only barely recognisable from Thiele's (1898) original description, in which specific details of its skeletal structure were missing. However, Thiele's illustrations of its spicules were adequate to indicate that it was most appropriately included in *Raspaxilla*. Recent recollections of the species from Japan and Korea provided additional skeletal details to confirm this placement.

**Raspailia (Raspaxilla) frondula**
(Whitelegge, 1907)
(Fig. 23)

*Axinella frondula* Whitelegge, 1907: 509-510, pl. 46, fig. 32.
*Echinaxia frondula*; Hallmann 1916a: 543; Hallmann 1917: 394-398, text-fig. 1, pl. 21, figs 3-4, pl. 22, figs 1-2.
*Raspailia frondula*; Bergquist 1970: 30.
*Raspailia* (*Raspaxilla*) *frondula*; Hooper, 1991: 1248, fig. 34

MATERIAL. HOLOTYPE. AM G4349: Shoalhaven Bight, S coast of NSW, 34° 51'S, 150° 45'E, 60 m depth, coll. 'Thetis'.

DISTRIBUTION. Shallow coastal waters of S NSW, Australia.

DESCRIPTION. Stalked branching flabellate growth form. Surface with fine, close-set microconules. Colour light brownish-grey in ethanol. 'Raspailiid ectosomal skeleton' absent, although long subectosomal extra-axial styles form plumose brushes around terminal portions of ascending peripheral fibres, protruding through the surface and producing distinctive surface conules. Axial and extra-axial skeletons moderately well-differentiated. Axial skeletal slightly compressed, with the axial core composed of very light spongin fibres, forming an irregular subrenieroid reticulation cored by pauci- or multispicular longitudinal tracts and interconnected by uni- or paucispicular transverse tracts of choanosomal principal styles. Extra-axial skeleton composed of prominently radial, non-plumose bundles of choanosomal principal styles arising perpendicular to axis, without interconnecting reticulate tracts. Echinating acanthostyles slightly more abundant in peripheral skeleton than in axis. Megascleres include choanosomal principal styles, short, thin, slightly curved at centre or towards basal end, occasionally oxeote or strongylote, with rounded non-tylote bases, without basal rhabd, and with slightly hastate points (87-165×3-8μm). Echinating rhabdostyles short, thin, with smooth, slightly swollen, rhabdose bases and distal (pointed) 2/3 of spicule evenly covered with vestigial spines (72-133×4-9μm). Subectosomal extra-axial styles long, slightly curved towards basal end, with rounded non-tylote bases (278-710×4-16μm). Ectosomal auxiliary megascleres absent. Microscleres absent.

REMARKS. This species differs from most *Raspaxilla* in having radial, non-plumose tracts of choanosomal principal styles and subectosomal extra-axial styles forming the ascending fibres in the peripheral skeleton, and lacking any reticulate connections between adjacent radial tracts; lacking the special ectosomal auxiliary spicules characteristic of raspailiids; having a wide-meshed reticulation in the axial skeleton (less compressed than most species of *Raspaxilla*); and having choanosomal principal styles (coring axial fibres) of similar size to echinating rhabdostyles, differing only in their thickness, hastate points and entirely smooth surface. Hallmann (1917) suggested that choanosomal principal (coring) and echinating spicules in *R. frondula* may have a common origin, as indicated by their similar size, similar to those found in species of *Aulospongus*. However, the respective geometries of these

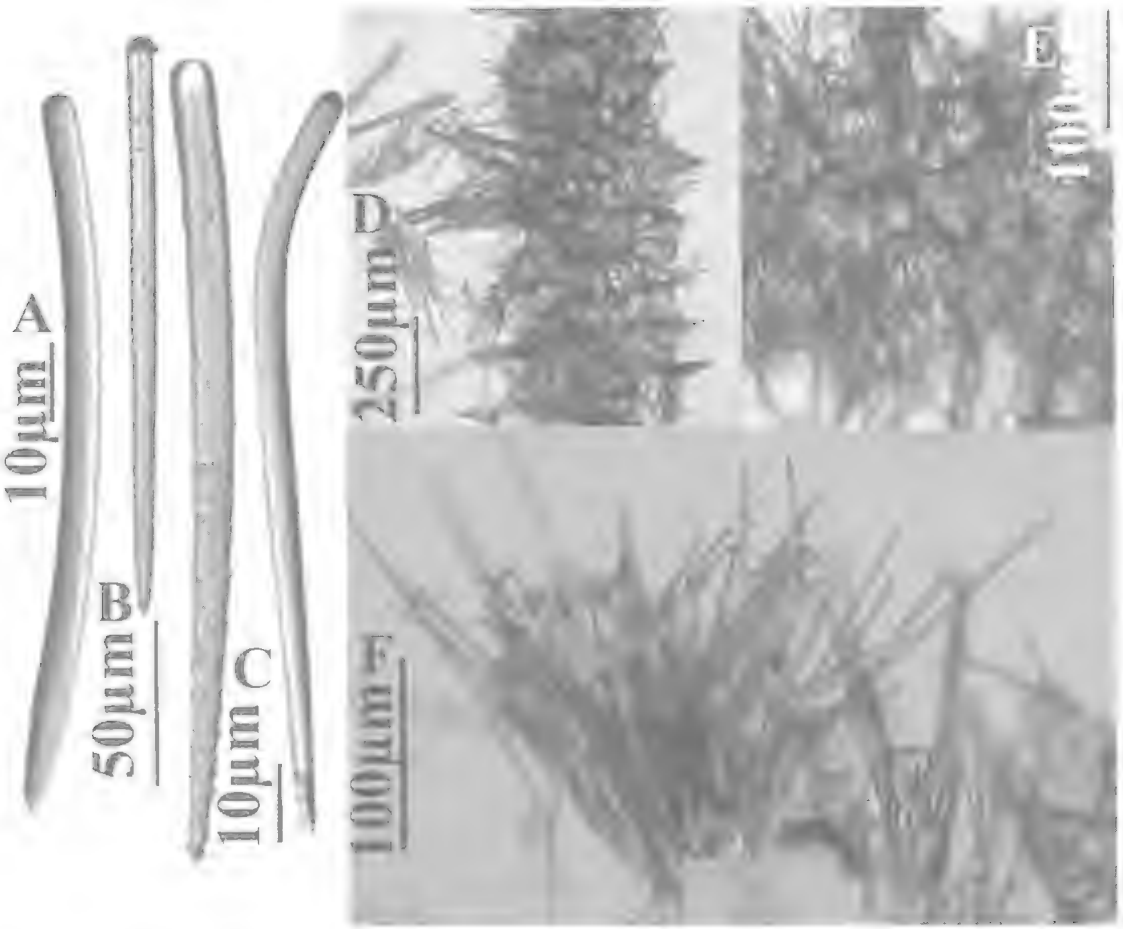



FIG. 23. *Raspailia (Raspaxilla) frondula.* A, Choanosomal principal style. B, Subectosomal extra-axial style. C, Echinating rhabdostyles. D, Skeletal cross-section through branch. E, Reticulate axial skeleton. F, Ectosomal spicule bundle composed of subectosomal extra-axial styles.

spicules appear to be different and this proposed relationship is not supported: coring styles are nearly hastate-pointed with curvature closer to the centre (including occasional oxeote/strongylote forms), whereas echinating rhabdostyles are tapering fusiform-pointed, with slightly swollen bases and slight to moderate basal rhabds.

**Raspailia (Raspaxilla) galapagensis**
(Desqueyroux-Faundez & van Soest, 1997)
(Fig. 24)

*Aulospongus galapagensis* Desqueyroux-Faundez & van Soest, 1997: 441, figs 165-168.

MATERIAL. HOLOTYPE. USNM43173 (fragment ZMA POR11241): Albemarle I., Galapagos Is, 00°37'S, 90°51'W, coll. 'Anton Bruun', 1966, 78m depth.

DISTRIBUTION. Known only from the Galapagos Is.

DESCRIPTION. Growth form branching. Surface highly hispid. Colour beige in ethanol. 'Raspailiid ectosomal skeleton' present consisting of a central long subectosomal extra-axial style surrounded by small ectosomal auxiliary styles/anisoxeas in large bundles at the surface. Axial and extra-axial skeletons well differentiated. Axial skeleton consists of a well compressed, close-meshed reticulation of long choanosomal principal styles running mainly longitudinally through branches, with fewer transverse interconnecting fibres, with compression so strong that reticulate fibres are often masked. Extra-axial skeleton reduced to single long subectosomal extra-axial styles embedded

in, and perpendicular to, axis. Echinating rhabdostyles localised at the junction of axial and extra-axial skeletons, outside and perpendicular to the axis, extending up to and occasionally through the surface, usually occurring singly. Megascleres consist of entirely smooth choanosomal principal styles, oxeas, stongyles or strongylostyles, without any obvious basal rhabd, slightly curved centrally or with curvature closer to the basal end (400-1700×20-45μm). Echinating rhabdostyles with slight to moderate basal rhabd (very occasionally completely smooth), bases mostly smooth and slightly subtylote, with moderately large recurved spines confined to the apex, occasionally also spined on the base (170-320×15-30μm). Subectosomal extra-axial styles very long, slightly curved near base, also with strongylostylote modifications (1300-1700×20-45μm). Ectosomal auxiliary styles/anisoxeas relatively large, thick, straight, very slightly curved at centre or exceptionally sinuous, usually asymmetrical with one blunt end, sometimes symmetrical, oxeote (450-550× 8-15μm). Microscleres absent.

REMARKS. This species is referred here to *Raspailia* (*Raspaxilla*) on the basis that its choanosomal principal styles are morphologically very different from echinating rhabdostyles, lacking any traces of basal rhabds, and moreover they are frequently modified to strongylote or oxeote forms; there are no fibre-bundles characteristic of *Aulospongus*, instead the axial and extra-axial skeletons are well differentiated, with the axis compressed and extra-axis reduced to radial single spicules; and echinating rhabdostyles form a dense perpendicular layer at the surface, outside the axial skeleton.

The species is distinctive in the very large size and robust nature of its spicules. Desqueyroux-Faundez & van Soest (1997) suggested that *R.* (*R.*) *galapagensis* was most similar to, and possibly conspecific with, *R.* (*R.*) *hyle*, with apparent notable differences being a branching growth form (versus frondose, vasiform), a prominently hispid surface (versus smooth), much larger ectosomal auxiliary styles/anisoxeas, and long subectosomal extra-axial styles perpendicular to the axis (supposedly absent in *R.* (*R.*) *hyle*). However, re-examination of respective holotypes found that *R.* (*R.*) *hyle* has substantially smaller choanosomal principal styles than *R.* (*R.*) *galapagensis*; long subectosomal extra-axial styles are definitely present in *R.* (*R.*) *hyle* with only a few erect on the surface (the remainder confined within the mesohyl); ectosomal auxiliary styles/anisoxeas do not form characteristic raspailiid surface brushes in *R.* (*R.*) *hyle* but are scattered within the peripheral skeleton, entirely within the mesohyl; the surface in *R.* (*R.*) *hyle* is conulose and shaggy; and rhabdostyles have a substantially different morphology between the two species (see Figs 24-25).

**Raspailia (Raspaxilla) hirsuta** Thiele, 1898

*Raspailia hirsuta* Thiele, 1898: 59, pl. 3, fig. 9, pl. 8, fig. 46a-d; Tanita, 1961: 344, fig. 4, pl. 3, fig. 10; Tanita, 1970: 102, pl. 2, fig. 8; Hoshino, 1971: 24; Hoshino, 1975: 32, pl. 4, figs 8-9; Hoshino, 1981: 216-218, fig. 8; Hoshino, 1987: 18; Sim & Kim, 1988: 28; Tanita & Hoshino, 1990: 100, text-fig. 62; Sim, 1990: 317.
*Echinaxia hirsuta*; Hallmann, 1917: 392.
*Raspailia* (*Raspaxilla*) *horsuta* [sic.]; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE. ZMB (not seen): Sagami Bay, Japan.

DISTRIBUTION. Japan (Sagami Bay, Kii Channel, Seto Inland Sea) and Korea (Chejudo, South Sea coast, Jeju I.).

DESCRIPTION. Growth form erect, irregularly digitate, foliose lamellae, branches flattened and irregularly bulbous. Surface minutely conulose and hispid. Colour orange or pinkish-brown alive. 'Raspailiid ectosomal skeleton' present but rudimentary, composed of vestigial raphide-like anisoxeas, and larger subectosomal extra-axial styles protruding through surface. Axial and extra-axial skeletons moderately well differentiated. Axial skeleton composed of a network of heavy fibres cored by smaller choanosomal principal styles, abundantly echinated by rhabdostyles. Extra-axial skeleton composed of fibres cored by longer subectosomal extra-axial styles extending radially from the axis all the way to the periphery and projecting through the surface. Megascleres include choanosomal principal styles, slender, slightly curved at centre or towards base, entirely smooth, without basal rhabd (405-(787)-1015× 9-(18)-40μm). Echinating rhabdostyles relatively long, thick, base smooth with moderate to well developed basal rhabd, small granular spines on apical half or 2/3 of spicule (210-(282)-390×8-(12)-14μm). Subectosomal extra-axial styles rare, long, thick, straight or slightly curved towards base, occasionally strongylote (250-(495)-800× 3-(4.6)-8μm). Ectosomal auxiliary oxeas or anisoxeas, raphidiform, slightly sinuous, tapering from the middle to each end, with asymmetrical points (140-(252)-400×

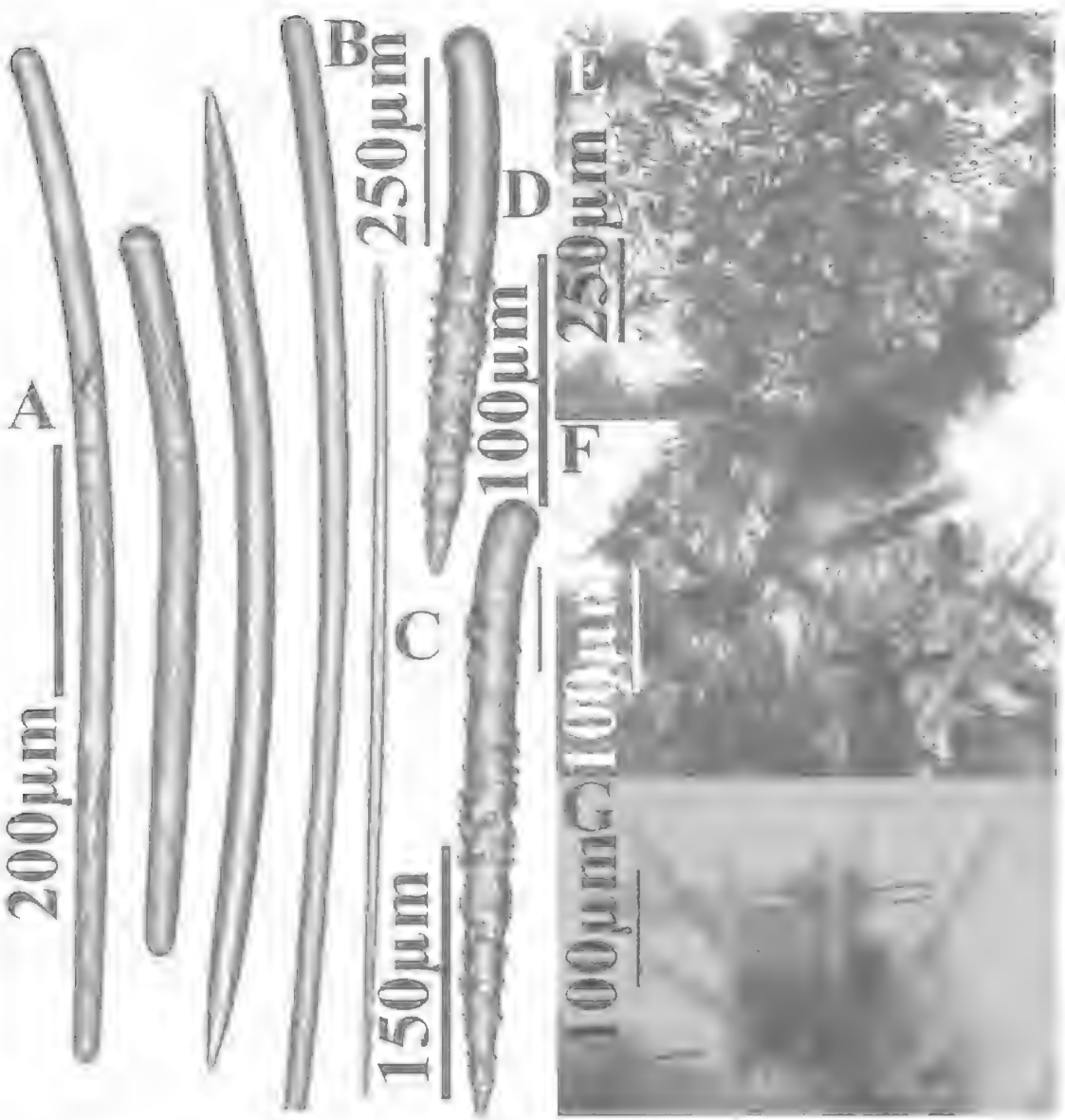



FIG. 24. *Raspailia (Raspaxilla) galapagensis*. A, Choanosomal principal strongylostyles and oxea. B, Basal end of subectosomal extra-axial style. C, Ectosomal auxiliary anisoxea. D, Echinating rhabdostyles. E, Compressed reticulate axial skeleton. F, Rhabdostyles in extra-axial skeleton. G, Ectosomal skeleton.

1-(2)-3µm). Microscleres absent (Thiele, 1898; Tanita, 1961; Hoshino, 1981; Sim, 1990: 317).

REMARKS. Thiele's (1898) original description of *R. (R.) hirsuta* was incomplete, providing only cursory information on ectosomal and choanosomal skeletal structure or spicule localisation, and the type material is currently missing (not located in the ZMB during a search by the author and Dr D. Kühlmann in 1988). Fortunately, newer material described from Japanese and Korean waters provides more precise details on external, skeletal and spicule morphologies, and the above description was compiled from this literature.

### Raspailia (Raspaxilla) hyle
(de Laubenfels, 1930)
(Fig. 25)

*Hemectyon hyle* de Laubenfels, 1930: 28; 1932: 107, fig. 64; Dickinson, 1945: 21, pl. 31, figs 61-62, pl. 32, figs 63-64; Bakus & Green, 1987: 79; Green & Bakus, 1994: 37-39, fig. 20.
*Aulospongus hyle*: Desqueyroux-Faundez & van Soest, 1997: 442.

MATERIAL. HOLOTYPE. USNM21418 (fragment BMNH1929.9.30.4): Point Fermin, San Pedro, California, coll. USC, 16.ii.1924, 30-150m depth.

DISTRIBUTION. Queen Charlotte Is, British Columbia, Canada to Tanner Bank, California coast, Gulf of California, Mexico.

DESCRIPTION. Growth form frondose, vasiform. Surface smooth. Colour pale drab in ethanol. 'Raspailiid ectosomal skeleton' vestigial, with ectosomal auxiliary styles/anisoxeas scattered on or below the surface, usually in bundles parallel to the surface, not forming brushes and not associated with protruding erect subectosomal extra-axial styles. Axial and extra-axial skeletons well differentiated. Axial skeleton more-or-less a loose-meshed reticulation of multispicular fibres cored by smooth choanosomal principal styles enclosed within light spongin fibres forming a nearly halichondroid criss-cross reticulation. Extra-axial skeleton consists of erect subectosomal extra-axial styles perpendicular to axis, protruding through the surface, and also lying parallel to the surface within the mesohyl, with a dense layer of erect rhabdostyles embedded and perpendicular to the axial skeleton, not protruding through the surface. Megascleres consist of slender, entirely smooth choanosomal principal styles, sometimes modified to strongyles, with curvature varying from slight to greatly curved, curvature central or slightly basal, without any basal rhabd (322-585×12-190μm). Echinating rhabdostyles with slight to moderate basal rhabd, sometimes completely straight, base slightly subtylote, entirely smooth on basal half with large, erect, slightly recurved spines sparsely scattered on apical (pointed) half of spicule (155-364×9-22μm). Subectosomal extra-axial styles long, slender, straight or slightly curved near basal end, occasionally strongylote (715-1650×9-16μm). Ectosomal auxiliary styles, or less commonly anisoxeas, raphidiform, curved in basal third or sinuous (165-385×0.8-1.5μm). Microscleres absent.

REMARKS. The species has been discussed above in comparison with *R.* (*R.*) *galapagensis*. De Laubenfels (1930, 1932) and Dickinson (1945) recorded raphides in their material but these are vestigial ectosomal auxiliary styles/anisoxeas. Several other inconsistencies between the type material and original descriptions have been corrected in the redescription above.

De Laubenfels (1932) originally included this species in *Hemectyon* on the basis of its allegedly strong similarities with the type species, *Hemectyon lumatum* (Schmidt, 1870): viz. possession of rhabdostyles with strongly recurved spines more-or-less restricted to the apex of spicules; localisation of echinating rhabdostyles to the peripheral skeleton; and 'unusual' axial core of styles enclosed in spongin (although this is now widely known to occur throughout the Raspailiidae). However, the resemblance between these two species is minimal: they are neither closely related nor does this species belong in *Endectyon* (*Hemectyon*). Desqueyroux-Faundez & van Soest (1997) subsequently referred *H. hyle* to *Aulospongus* based on its similarities with *R.* (*R.*) *galapagensis* (although these similarities are also only very slight; see remarks for *R.* (*R.*) *galapagensis*), whereas it is suggested here that both these species are more appropriately included in *Raspailia* (*Raspaxilla*).

### Raspailia (Raspaxilla) hymani
(Dickinson, 1945)
(Fig. 26)

*Hemectyon hymani* Dickinson, 1945: 21, pl. 33, figs 65-66; Green & Bakus, 1994: 39-40, fig. 21.
*Aulospongus hymani*: Desqueyroux-Faundez & van Soest, 1997: 442.

MATERIAL. HOLOTYPE. AHF no.10 (not seen): San Jaime Banks, Cabo San Lucas, Mexico, 22°50'N, 110°15'W, coll. 'Velero III', 3.iii.1937, 150m depth.

DISTRIBUTION. California to Cape San Lucas, Gulf of California, Mexico.

DESCRIPTION. Growth form flabellate, reticulate branching. Surface slightly hispid. Colour light drab, almost white, in ethanol. 'Raspailiid ectosomal skeleton' vestigial, with raphidiform ectosomal auxiliary styles/anisoxeas forming sparse brushes or scattered below the surface, but not necessarily surrounding the protruding spicules. Axial and extra-axial skeletons well differentiated. Axial skeleton composed of a highly compressed solid core of choanosomal principal styles aligned longitudinally through branches. Extra-axial skeleton plumo-reticulate composed of tracts of choanosomal principal styles embedded in axis and protruding at right angles through the surface, echinated on their outer edge by

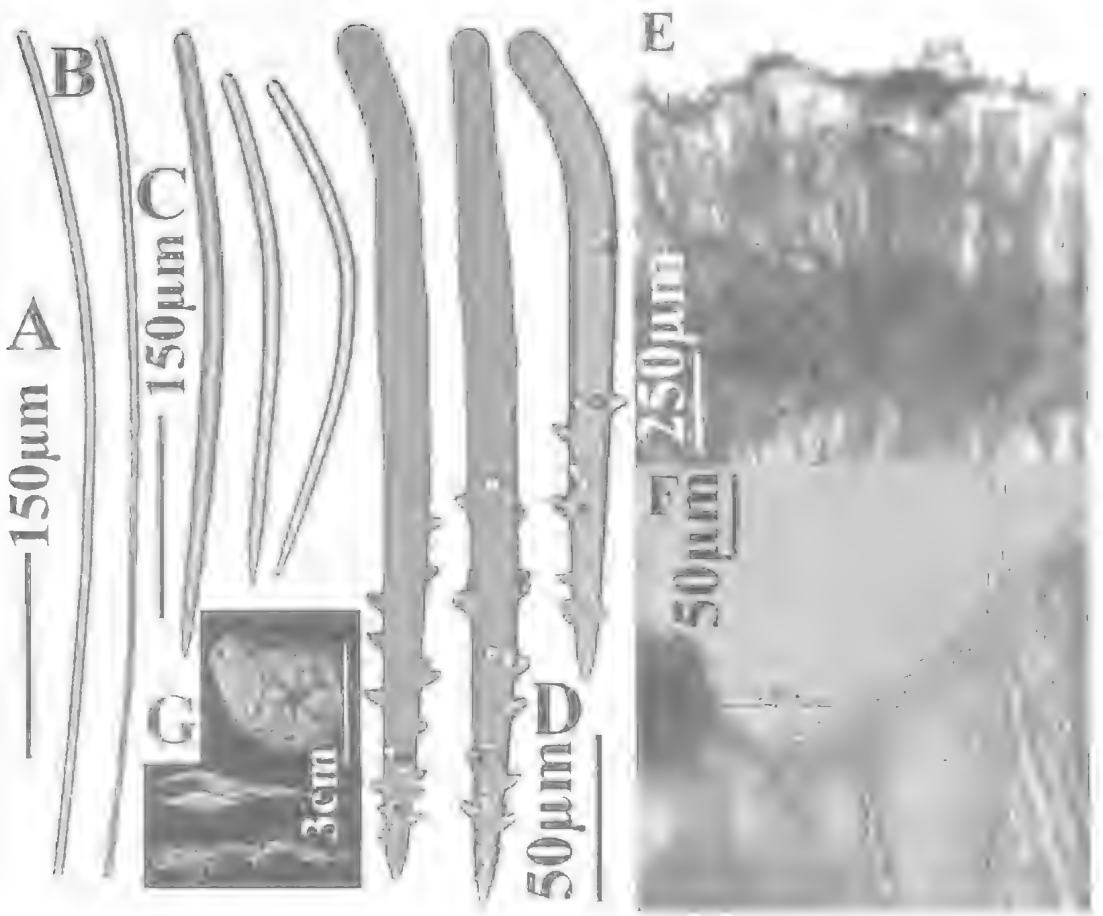



FIG. 25. *Raspailia (Raspaxilla) hyle*. A, Basal portion of subectosomal extra-axial style. B, Basal portion of ectosomal auxiliary style. C, Choanosomal principal styles. D, Echinating rhabdostyles. E, Axial and extra-axial skeletons. F, Ectosomal skeleton. G, Specimens AHF (modified from Dickinson, 1945).

rhabdostyles. Echinating rhabdostyles predominant in peripheral skeleton. Megascleres consist of long, smooth choanosomal principal styles, straight or slightly curved, entirely smooth, without any basal rhabd (650->1700×12-36µm). Echinating rhabdostyles with basal rhabd varying from slight to well curved, bases entirely smooth, with large recurved spines only on the apical half of spicule, sometimes modified to acanthotylostyles (130-300×6-30µm). Subectosomal extra-axial spicules absent. Ectosomal auxiliary styles/anisoxeas raphidiform (dimensions unknown). Microscleres absent (Dickinson, 1945; Green & Bakus, 1994).

REMARKS. This species has been recorded only twice, and regrettably the holotype cannot be located in the AHF collections (Prof. G. Bakus, pers.comm.). From its published descriptions the species has a distinctive reticulate-branching, flabellate growth form resembling *Echinodictyum cancellatum* (Lamarck) (Raspailiidae) and *Clathria coppingeri* (Ridley) (Microcionidae). It is assigned here to *Raspailia* (*Raspaxilla*) in having coring and echinating spicules of different morphology; echinating rhabdostyles localised outside the axis, perched on the junction of the axial and extra-axial skeletons; having well differentiated axial and extra-axial skeletons; and lacking the characteristic fibre-bundles found in *Aulospongus*. The E Pacific species *R.* (*R.*) *hymani*, *R.* (*R.*) *hyle* and *R.* (*R.*) *galapagensis* are similar in many of their characteristics and probably represent allopatric sibling species, analogous to the relationship between the sister species *R.* (*R.*) *clathrioides*, *R.* (*R.*) *reticulata* and *R.* (*R.*) *topsenti* from the SW. Pacific.

Green & Bakus (1994) briefly decribe two other unnamed species under *Hemectyon*, both similar to *R. hymani* but differing in several features. The status of these species is still uncertain, but it is possible that they are variable populations of *R. hymani*.

**Raspailia (Raspaxilla) inaequalis**
Dendy, 1924

*Raspailia inaequalis* Dendy, 1924: 355, pl. 12, fig. 1, pl. 14, figs 17-19; Bergquist, 1970: 28, fig. 2.
*Raspailia (Raspaxilla) inaequalis*; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE: BMNH1923.10.1.138 (not seen), North Cape, New Zealand, 140m depth, coll. 'Terra Nova'.

DISTRIBUTION. Known only from N New Zealand.

DESCRIPTION. Growth form digitate, stalked, thinly cylindrical, bifurcate branches. Surface granular, velvety, finely hispid. Colour greyish in ethanol. 'Raspailiid ectosomal skeleton' absent, although bundles of longer subectosomal extra-axial styles protrude slightly through the surface. Axial and extra-axial skeletons well differentiated. Axial skeleton compressed with dense reticulation of thick fibres cored by choanosomal principal styles, appearing almost disorganised halichondroid, with fibres only lightly echinated by rhabdostyles in axis. Extra-axial skeleton plumoreticulate, dominated by ascending, plumose, multispicular columns of choanosomal principal styles, columns embedded in and perpendicular to axis, interconnected by pauci- or unispicular transverse fibres extending all the way to the surface, ending in bundles of larger subectosomal extra-axial styles embedded in peripheral fibres. Ascending fibres in peripheral skeleton echinated by rhabdostyles, singly or in plumose bundles. Megascleres consist of slender choanosomal principal styles, centrally curved, entirely smooth, with evenly rounded base (220×5μm). Echinating rhabdostyles with moderate basal rhabd, smooth base, and small granular spines on apical 2/3 of spicule (130×8μm). Subectosomal extra-axial styles thick, relatively short, centrally curved, with evenly rounded base and hastate point (370-480×14-17μm). Special category of ectosomal auxiliary spicules absent. Microscleres absent (Dendy, 1924; Bergquist, 1970).

REMARKS. The species clearly belongs to *Raspaxilla* in its skeletal structure (well differentiated axial and extra-axial skeletons, compressed axis, plumoreticulate extra-axis) and

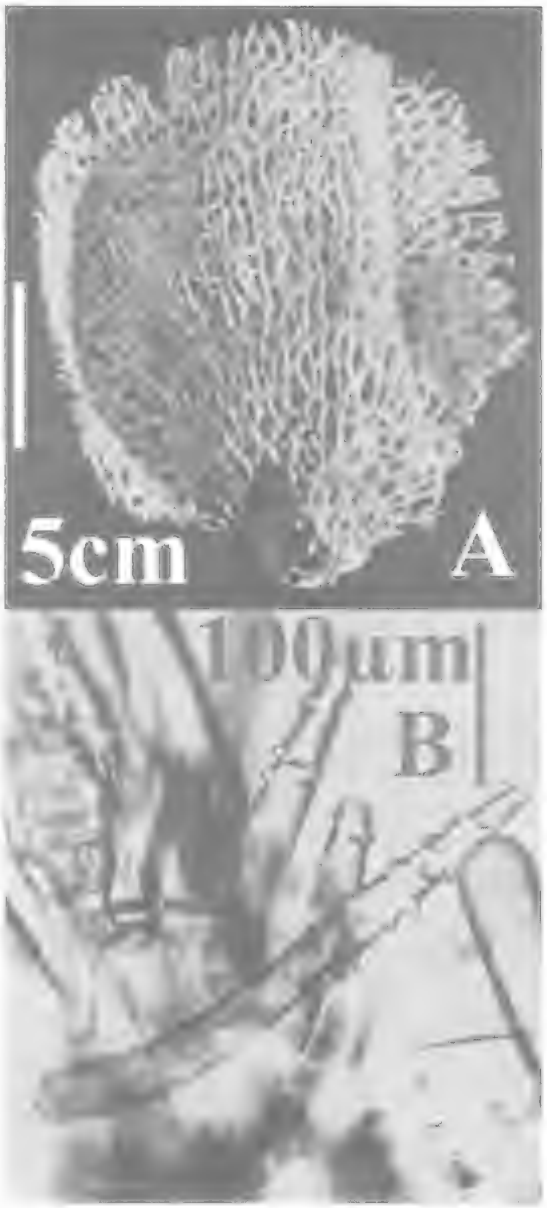



FIG. 26. *Raspailia (Raspaxilla) hymeni*. A, Holotype. B, Echinating rhabdostyles (figure modified from Dickinson, 1945).

spicule morphology (non-rhabdose choanosomal principal styles), although it lacks specialised ectosomal auxiliary spicules and there is little differentiation between choanosomal principal and subectosomal extra-axial styles. In some respects it is similar to *R.* (*R.*) *wardi* from Western Australia in spicule morphology and ectosomal features, whereas the two species

differ substantially in their growth form, surface features, density and location of echinating spicules, and spicule sizes.

### Raspailia (Raspaxilla) mariana
(Ridley & Dendy, 1886)
(Fig. 27)

*Axinella mariana* Ridley & Dendy, 1886: 480; 1887: 180, pl. 34, fig. 1, pl. 40, fig. 2; Koltun, 1964: 83, pl. 13, figs 7-10.
*Axinectya mariana*; Hallmann, 1917: 393.
*Raspailia* (*Raspaxilla*) *mariana*; Hooper, 1991: 1196, fig. 7d-f.

MATERIAL. HOLOTYPE. BMNH1887.5.2.28: Marion I., Prince Edward Islands, subantarctic, 100-150m depth, coll. 'Challenger'.

DISTRIBUTION. Known only from the subantarctic islands.

DESCRIPTION. Arborescent, bifurcate branching, flattened branches. Surface prominently hispid. Colour greyish-yellow in ethanol. 'Raspailiid ectosomal skeleton' absent, although extremely long subectosomal extra-axial styles protrude through the surface, singly or in bundles, surrounded by plumose brushes of rhabdostyles at their point of insertion through the surface. Axial and extra-axial skeletons well differentiated. Axial skeleton greatly compressed, heavy fibres, without any coring spicules but with the bases of long subectosomal extra-axial styles embedded. Extra-axial skeleton radial, with long subectosomal extra-axial styles radiating from the axis to the surface, surrounded along most of their length (within the sponge body) by echinating rhabdostyles in plumose bundles. Megascleres consist only of two forms. Principal spicules absent. Echinating rhabdostyles moderately thick, with smooth non-tylote base, basal rhabd varying from slight to well developed (strongly curved), and either completely smooth point or with small granular spines covering apical 2/3 of spicule (185-370× 8-18μm). Subectosomal extra-axial styles long, thick or slender, slightly curved near the basal end, slightly subtylote, completely smooth (1550-2400×12-29μm). Ectosomal auxiliary megascleres absent. Microscleres absent.

REMARKS. This species is unusual amongst *Raspaxilla* in lacking principal spicules completely, having only long subectosomal extra-axial styles radially oriented and embedded within axial fibres (i.e. no reticulate connecting tracts), and plumose bundles of echinating rhabdostyles throughout the axial and extra-axial skeletons. The absence of principal spicules makes it difficult to determine whether it belongs to *Aulospongus* (principal spicules with basal rhabds) or *Raspaxilla* (without basal rhabds), whereas the possession of a compressed axis and absence of fibre-bundles suggests it belongs to the latter genus. The species is a highly reduced *Raspaxilla* (also lacking specialised ectosomal auxiliary spicules).

### Raspailia (Raspaxilla) pearsei
(Wells, Wells & Gray, 1960)

*Hemectyon pearsei* Wells, Wells & Gray, 1960: 218, figs 14,26.

MATERIAL. HOLOTYPE. USNM 23651 (not seen): off Beaufort, North Carolina, 5m depth.

DISTRIBUTION. Known only from E coast USA.

DESCRIPTION. Small ellipsoidal mass composed of many compressed vertically elongated lamellae, 30mm long, 20mm high, encrusting rock. Texture stiff. Surface with many upright ridges 1-1.5mm apart, hispid particularly on ridges, with glabrous ectosomal membrane stretched between adjacent ridges. Colour unknown. Oscules up to 0.6mm diameter scattered over ectosomal membrane. Ectosomal specialisation unknown. Choanosomal skeleton composed of a axial reticulation of vertical and radial spongin fibres cored by choanosomal principal subtylostyles and echinated by rhabdostyles, with radial fibres and choanosomal principal spicules forming plumose bundles at the surface. Megascleres include choanosomal principal subtylostyles, entirely smooth, slightly curved at centre, with prominent tylote base and lacking any basal rhabd (190-340×10-14μm). Echinating rhabdostyles with prominent basal rhabd, entirely spined or with smooth base (85-115×3-7μm). Subectosomal extra-axial spicules not recorded. Ectosomal auxiliary spicules not recorded. Microscleres absent (Wells, Wells & Gray, 1960).

REMARKS. The type material of this species has not been re-examined, and it is only known so far from its original description. The true nature of its ectosomal and choanosomal skeletal structures is still uncertain, and it is possible that ectosomal auxiliary spicules and/or subectosomal extra-axial spicules were overlooked by Wells et al. (1960), or that it is indeed a very reduced species in it spicule complement. From its description it appears to conform best to

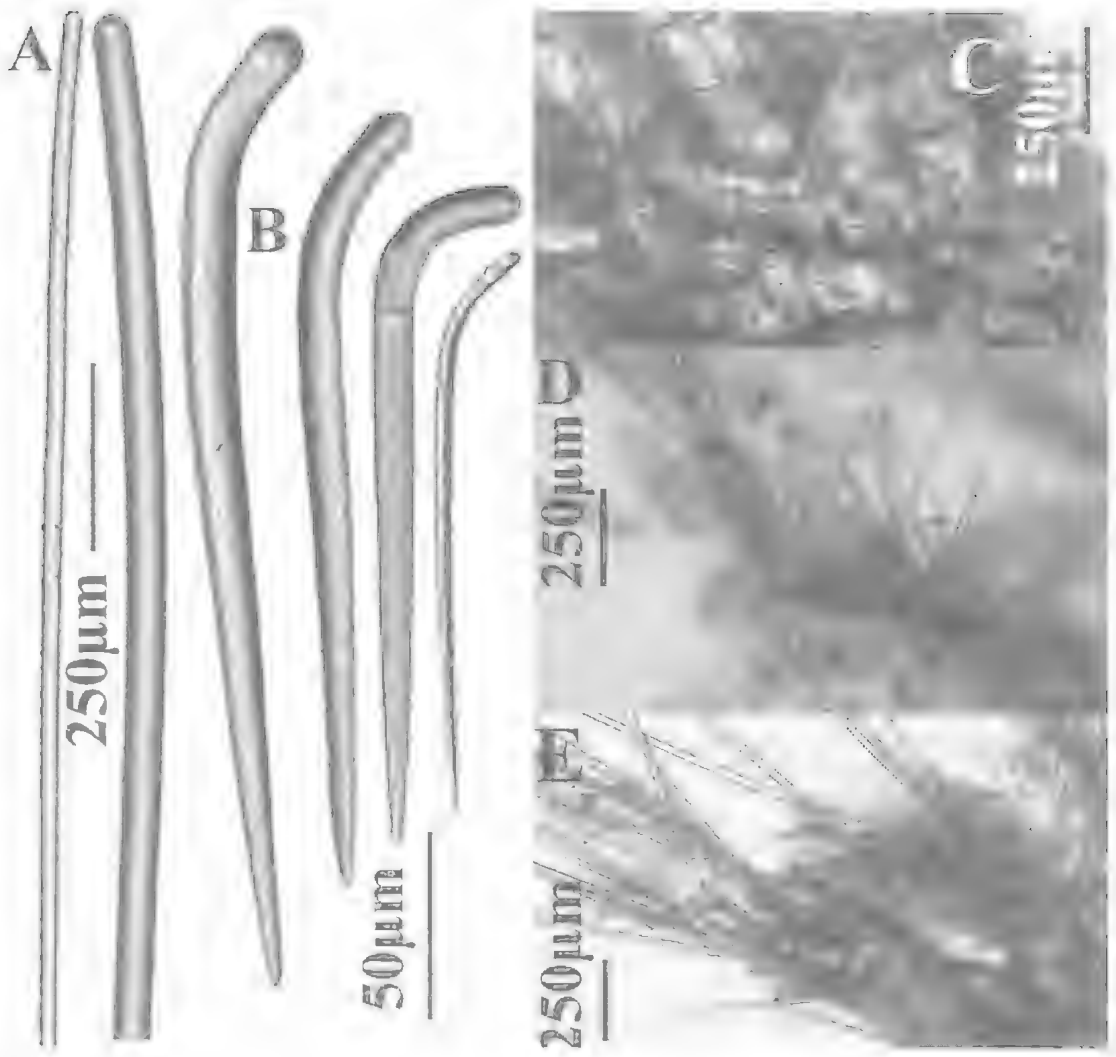



FIG. 27. *Raspailia (Raspaxilla) mariana*. A, Basal portion of subectosomal extra-axial styles. B, Echinating rhabdostyles. C, Reticulate axial skeleton. D, Peripheral fibre. E, Ectosomal skeleton.

*Raspailia* (*Raspaxilla*) (i.e. choanosomal principal styles are morphologically very different from echinating rhabdostyles, entirely smooth and lacking any traces of basal rhabds; there are no fibre-bundles characteristic of *Aulospongus*; and skeletal structure apparently varies between axial and extra-axial regions). Wells et al. (1960) noted that *R. pearsei* resembles *R. hyle* to some extent, differing in the respective sizes of echinating rhabdostyles, but these affinities require confirmation from the type material.

**Raspailia (Raspaxilla) reticulata**
Hooper, 1991
(Figs 28-29, 36D)

*Raspailia (Raspaxilla) reticulata* Hooper, 1991: 1250, figs 35-36.

MATERIAL. HOLOTYPE. QMGL1982: Green I., Cairns Section, Great Barrier Reef, 16°46'S, 145°58'E. OTHER MATERIAL. QMG307874, QMG313312: Wooded Islet, Low Isles, Cairns Section, GBR, 16°23.7'S, 145°34.3'E, 24m depth, 18.i.1997, coll. 'Gwendolyn May'.

DISTRIBUTION. Known only from the N Great Barrier Reef.

DESCRIPTION. Erect, arborescent, stalked, cylindrical branches, bulbous nodes. Surface finely conulose, fleshy, hispid, slightly shaggy. Colour yellow-orange (Munsell 2.5Y 8/10) alive. Oscules very small (<1mm diameter), slightly raised above the surface with membranous lip when alive, with small surface drainage canals radiating towards oscules. Texture stiff (basal stalk), flexible (branches), fleshy when alive. Ectosome hispid, moderately collagenous, with darkly pigmented collagen layer up to 200µm thick. Specialised 'raspailiid ectosomal skeleton' present, consisting of long thin subectosomal extra-axial styles and stout choanosomal principal styles protruding through surface in small bundles of 2-5 spicules, or singly, surrounded at their bases by ectosomal auxiliary anisoxeas, which form large bundles in plumose, radial or clumped-sinuous tracts. Projecting ectosomal and subectosomal spicules extend up to 500µm from the surface, producing irregularly spaced, long, slender conules. Collagenous component of conules extends 100-350µm from the surface. Axial and extra-axial skeletons only slightly differentiated. Axial skeleton predominantly reticulate, only slightly compressed, with relatively tight meshes formed by well developed spongin fibres (35-70µm diameter), bulbous at fibre nodes (up to 90µm diameter), forming elongate-oval meshes (150-320µm long, 90-140µm wide), with abundant granular collagen within mesohyl; fibre size relatively homogeneous throughout axial skeleton, although ascending fibres are cored by paucispicular tracts of 2-3 choanosomal principal styles and transverse fibres are aspicular or unispicular. Extra-axial skeleton plumo-reticulate, with skeletal tracts diverging as they ascend, becoming more plumose, with progressively fewer interconnecting tracts towards the peripheral skeleton, although interconnections between adjacent fibres persist all the way to the surface. Peripheral skeleton with pauci- or multispicular ascending fibres, cored by 2-5 choanosomal principal styles per tract; transverse connecting fibres are aspicular or unispicular. Coring styles in peripheral skeleton are generally larger than those in axial fibres. Echinating rhabdostyles more-or-less evenly scattered throughout the skeleton, perhaps slightly more dense at fibre nodes, protruding perpendicularly from fibres. Megascleres consist of larger choanosomal principal styles, entirely smooth, slightly curved at centre, with straight base or occasionally with a slight basal rhabd, bases evenly rounded, occasionally modified to strongylote forms (165-(344.1)-402×8-(10.6)-13µm). Smaller echinating rhabdostyles club-shaped, with prominent smooth subtylote base, with or without well-developed basal rhabd, spines granular, evenly dispersed but restricted to apical two-thirds of spicule (58-(80.3)-97×3-(6.6)-9µm). Subectosomal extra-axial styles very long, slender, entirely smooth, with variable shape ranging from slightly curved near basal end, straight, with several asymmetrical curves, sinuous or raphidiform (455-(726.7)-1025× 2-(6.4)-10µm). Ectosomal auxiliary anisoxeas raphidiform, slightly curved near basal end, asymmetrical ends with points tapering, fusiform and bases tapering, hastate, rounded, completely smooth (255-(325.3)-445× 1.5-(2.2)-3µm). Microscleres absent.

REMARKS. This species was known previously only from a single dead, trawled sample, with living populations recently discovered on the Low Isles providing additional characters for the species (hence redescribed in detail above; compare spicule measurements with those of Hooper, 1991: 1252). This species is a sister-species to (and potentially a synonym of), *R. (R.) clathrioides* (New Caledonia) and *R. (R.) topsenti* (N New Zealand), with observed differences significant certainly at the population level, but equivocally at the species level (refer to remarks under *R. (R.) clathrioides*).

**Raspailia (Raspaxilla) topsenti** Dendy, 1924
(Fig. 30)

*Raspailia topsenti* Dendy, 1924: 354, pl. 12, fig. 4, pl. 14, figs 14-16; de Laubenfels, 1936: 102; Bergquist, 1970: 28, fig. 3b, pls 6c-d, 7a, 10d, 18d, 19d.
*Raspailia (Raspaxilla) topsenti*; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE, BMNH1923.10.1.135: North Cape, New Zealand, 140m depth, coll. "Terra Nova".

DISTRIBUTION. Known only from N New Zealand.

DESCRIPTION. Arborescent, stalked, dichotomously branching, cylindrical branches. Surface granular, minutely hispid. Colour deep dull-orange alive. 'Raspailiid ectosomal skeleton' vestigial, with sparse, wispy ectosomal auxiliary styles/anisoxeas scattered on or below surface, singly or in sparse brushes. Axial and extra-axial skeletons moderately well differentiated. Axial skeleton compressed, close-meshed reticulation of heavy fibres cored by choanosomal principal styles, with few echinating spicules. Extra-axial skeleton

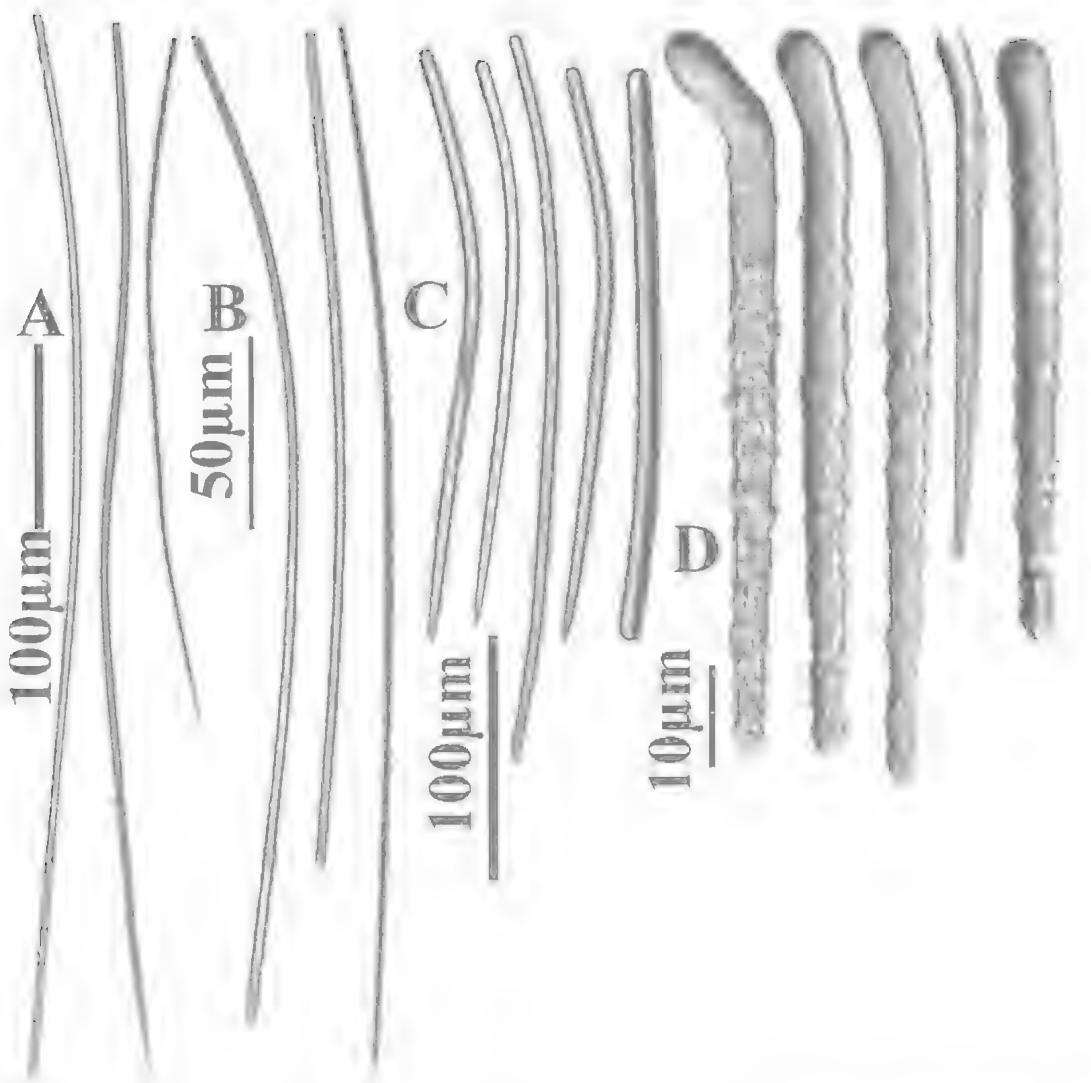



FIG. 28. *Raspailia (Raspaxilla) reticulata*. A, Subectosomal extra-axial styles. B, Ectosomal auxiliary anisoxeas. C, Choanosomal principal styles. D, Echinating rhabdostyles.

plumo-reticulate, with pauci- or multispicular tracts of choanosomal principal styles ascending to the surface (often protruding through fibres), interconnected by uni- or paucispicular tracts, abundantly echinated by rhabdostyles particularly close to surface. Megascleres include short, thick choanosomal principal styles, slightly curved at centre or towards base, sometimes straight, with evenly rounded smooth base, occasionally oxeote, with abrupt hastate points (265-474×12-21µm). Echinating rhabdostyles short, thick, with swollen, smooth, bulbous bases, basal rhabds ranging from slightly curved to prominently curved, with small granular spines on apical 3/4ths of spicule (68-125×7-10µm). No specialised subectosomal extra-axial spicules present. Ectosomal auxiliary styles or anisoxeas very thin, nearly raphidiform, straight, slightly curved or sometimes sinuous (185-245×1-2µm). Microscleres absent.

REMARKS. This species clearly belongs to *Raspaxilla* in having a compressed reticulate axial skeleton, a plumo-reticulate extra-axial skeleton, choanosomal principal styles lacking basal rhabds and of distinctly different morphology than echinating rhabdostyles, and lacking any sign of plumose fibre-bundles. It is

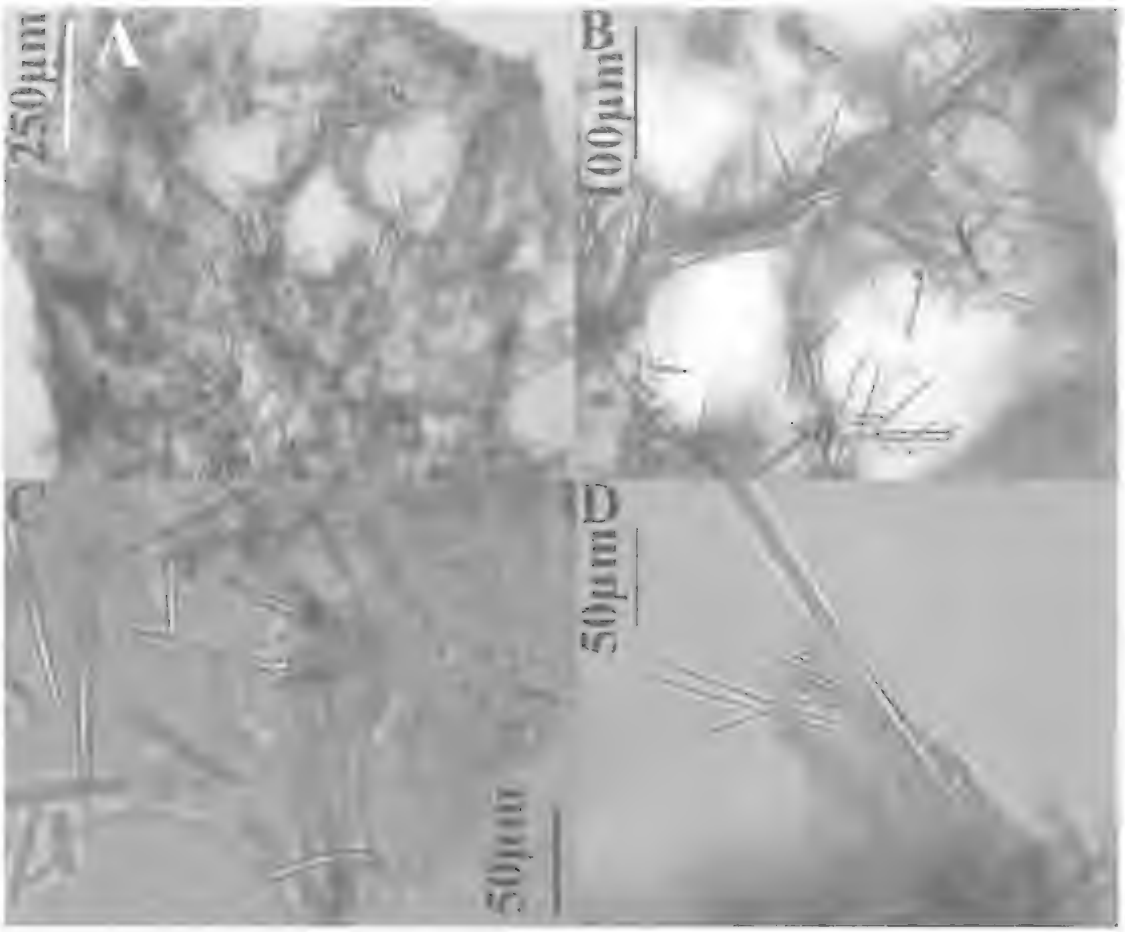



FIG. 29. *Raspailia (Raspaxilla) reticulata.* A, Reticulate choanosomal skeleton. B, Reticulate extra-axial skeleton. C, Choanosomal fibre. D, Ectosomal skeleton.

reduced in its ectosomal features, lacking any specialised subectosomal extra-axial spicules (i.e. undifferentiated from choanosomal principal spicules), and having only a vestigial specialised 'raspailiid ectosomal skeleton'. Based on rhabdostyle morphology (shape and spination) it is altogether most similar to *R.* (*R.*) *clathrioides* (New Caledonia) and *R.* (*R.*) *reticulata* (N Great Barrier Reef): the three species forming a sibling species group.

**Raspailia (Raspaxilla) wardi** Hooper, 1991
(Fig. 31)

*Raspailia* (*Raspaxilla.*) *wardi* Hooper, 1991: 1252, figs 37-38.

MATERIAL. HOLOTYPE. NTM Z1319: W of Port Hedland, Northwest Shelf, WA, 19° 03.5'S, 119° 03.6'E, 81 m depth, 28.iv.1983, coll. 'Soela'.

DISTRIBUTION. Known only from the Northwest Shelf, Western Australia.

DESCRIPTION. Thin, stalked, elongate, flabellate growth form. Surface smooth, microscopically very hispid. Colour bright red-orange alive. 'Raspailiid ectosomal skeleton' absent, although subectosomal extra-axial styles protrude a long way through the surface surrounded by bundles of echinating rhabdostyles standing perpendicular to the axial skeleton, forming tightly plumose brushes and producing a continuous subdermal palisade. Axial and extra-axial skeletal architecture markedly differentiated. Axial skeleton moderately compressed, composed of close-meshed, regularly renieroid reticulate fibres cored by uni- or paucispicular tracts of choanosomal principal styles. Extra-axial skeleton radial, with long subectosomal

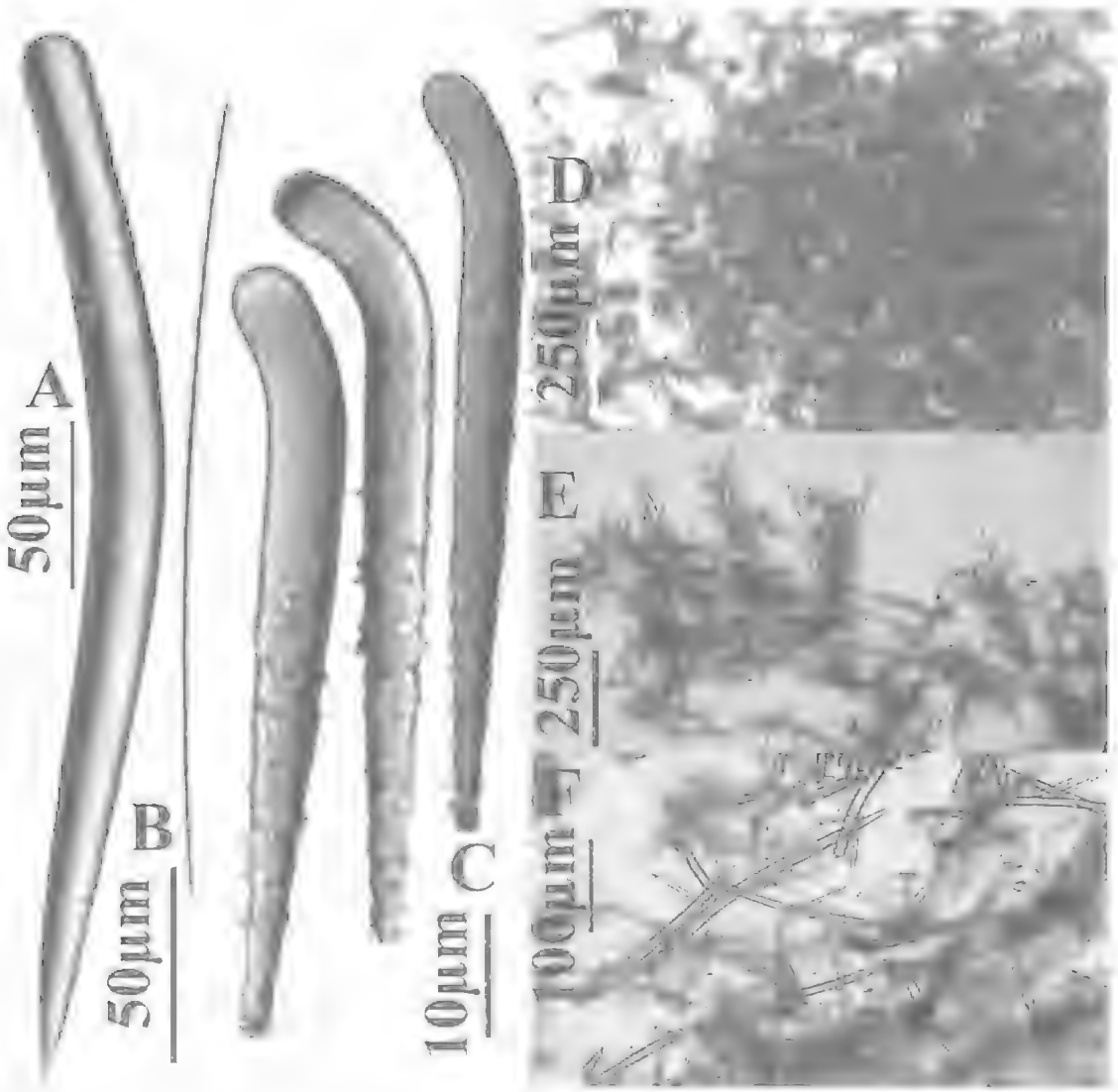



FIG. 30. *Raspailia (Raspaxilla) topsenti.* A, Choanosomal principal style. B, Ectosomal auxiliary anisoxea. C, Echinating rhabdostyles. D, Reticulate axial skeleton. E, Ectosomal skeleton. F, Extra-axial fibres.

extra-axial styles embedded in peripheral fibres and protruding through the surface. Echinating rhabdostyles absent from axial skeleton, occurring only as a palisade on the outer edge of the axis. Megascleres include choanosomal principal styles, rarely anisoxeas, entirely smooth, most slightly curved centrally towards basal end, with rounded non-tylote bases or very occasionally with slight basal rhabd (147-222×5-9µm). Echinating rhabdostyles thick, with basal rhabds ranging from slight to moderately curved, with a few basal spines but more heavily spined on apical part of spicule, spines small, recurved (112-165×8-12µm). Subectosomal extra-axial styles long, thick, slightly curved towards basal end or occasionally straight, with almost hastate points and rounded non-tylote bases (515-1122×7-16µm). Specialised ectosomal auxiliary spicules absent. Microscleres absent.

REMARKS. This species differs from most other *Raspaxilla* in its extremely thin flabellate growth form, renicroid reticulate axial skeleton, and possession of a continuous palisade of rhabdostyles on the ectosome, forming plumose brushes, but which are otherwise absent from the

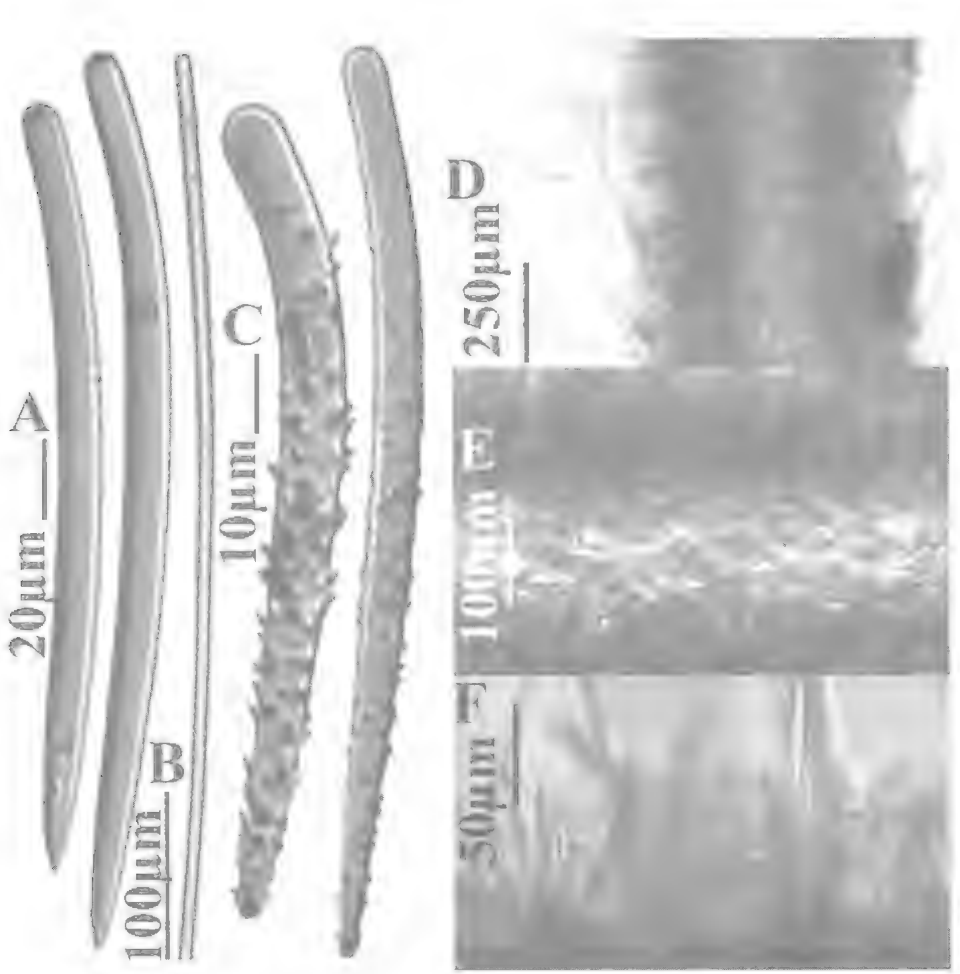



FIG. 31. *Raspailia (Raspaxilla) wardi*. A, Choanosomal principal styles. B, Basal portion of subectosomal extra-axial style. C, Echinating rhabdostyles. D, Skeletal cross-section through branch. E, Axial and extra-axial skeletons. F, Rhabdostyles in extra-axial skeleton.

axial skeleton. In this latter feature this species could arguably be included in *Endectyon* (*Hemectyon*) (see below), although in this case the localisation of rhabdostyles mainly on the surface is probably a function of the thin flabellate growth form, whereby the choanosomal skeleton is compacted and essentially the rhabdostyles are 'pushed' into the peripheral region. It is not included in *Endectyon* (*Hemectyon*) given the geometry and spination of rhabdostyles. It is included in *Raspailia* (*Raspaxilla*) as a reduced species, lacking specialised ectosomal auxiliary megascleres. In spicule morphology and spicule diversity it shows a closer relationship to *R.* (*R.*) *inaequalis* than to any other species.

**Endectyon** Topsent, 1920
Subgenus **Hemectyon** Topsent, 1920

*Hemectyon* Topsent, 1920: 27; Hooper, 1991: 1284. Type species *Raspailia* (?) *hamatum* Schmidt, 1870: 62, by original designation.

DEFINITION. *Endectyon* with echinating acanthostyles bearing clavulate spines only on apex of spicule, with smooth bases sometimes having a slight basal rhabd. Echinating spicules localised outside the axial skeleton, usually at the junction of axial and extra-axial skeletons, and/or forming plumose brushes along extra-axial skeleton, and often also producing spicule brushes at the surface. Axial skeleton compressed, reticulate. Extra-axial skeleton plumose or plumoreticulate cored by choanosomal principal styles.

REMARKS. *Hemectyon* was merged into synonymy with *Endectyon* by Hooper (1991), on the basis that the two differed in few characters. *Endectyon* (*s.s.*) has a specialised 'raspailiid ectosomal skeleton' composed of small ectosomal auxiliary styles/anisoxeas grouped around long subectosomal extra-axial styles. By comparison, *Hemectyon* lacks either of the special categories of ectosomal auxiliary or subectosomal extra-axial styles, and its ectosomal skeleton consists instead of acanthostyles grouped around protruding choanosomal principal styles. *Hemectyon* also has a more openly reticulate axial skeleton than does *Endectyon* (s.s.). More importantly though, in *Hemectyon* the bases of acanthostyles are predominantly smooth, subtylote, and some are slightly rhabdose, whereas those of *Endectyon* have recurved (clavulate) hooks on both ends and lack any basal rhabd. On this basis *Hemectyon* may be treated as a convenient subgenus within *Endectyon*, both having in common clavulate spines on acanthostyles, but in the latter genus these are localised outside the axial skeleton (usually at the junctions of axial and extra-axial skeletons).

Comparisons between *Endectyon* (*Hemectyon*) and *Aulospongus* and *Raspailia* (*Raspaxilla*) are slightly misleading. Echinating acanthostyles in *Endectyon* (*Hemectyon*) are not truly rhabdose, like the other two genera, with the slight basal curvature often overemphasised by the presence of a pronounced basal swelling on these spicules. Nevertheless, rhabdostyles in these three genera may be potentially confused. The subgenus contains only the type species, although arguably *E. fruticosa* (Dendy), *E. fruticosa aruensis* (Hentschel), and *E. xerampelina* (Lamarck) could also be included given that some (but not all) of their echinating acanthostyles have smooth, swollen, slightly rhabdose bases with clavulate spines mainly on the apex of the spicule. They are not included, however, because other spicules also have clavulate spines on their bases and more closely resemble those of *Endectyon* species (see Hooper, 1991).

**Endectyon (Hemectyon) hamatum**
Schmidt, 1870
(Fig. 32, Table 1)

*Raspailia ? hamata* Schmidt, 1870: 62; Desqueyroux-Faundez & Stone, 1992: 56.
*Hemectyon hamatum*; Topsent, 1920: 26, fig. 4a
*Endectyon hamata*; Hooper, 1991: 1284, fig. 53d-f (not Pulitzer-Finali, 1993: 307).

MATERIAL. HOLOTYPE. MZUS P0151 (fragment MNHN LBIM DT2161): 'West Indies'.

DISTRIBUTION. Caribbean.

DESCRIPTION. Growth form arborescent, cylindrical branches. Surface slightly corrugated. Colour pale brown in dry state. Specialised 'raspailiid ectosomal skeleton' absent, with only protruding bundles of a few choanosomal principal styles surrounded at their base by multispicular plumose bundles of rhabdostyles, although vestigial ectosomal auxiliary styles are scattered within the choanosomal skeleton. Axial and extra-axial skeleton moderately well differentiated. Axial skeleton strongly reticulate, compressed, with heavy fibres cored by small choanosomal principal styles in multispicular tracts mostly running longitudinally through branches, and with few echinating rhabdostyles. Extra-axial skeleton radial-reticulate, without fibre-bundles, with ascending paucispicular tracts interconnected by unispicular transverse tracts of choanosomal principal styles. Echinating rhabdostyles predominantly on exterior surface of primary (ascending) extra-axial fibres, with greatest numbers concentrated at the surface in brushes. Megascleres consist of choanosomal principal styles slightly curved centrally, without basal rhabd, entirely smooth (270-615×8-18μm). Echinating rhabdostyles with very slight basal rhabd, smooth slightly swollen base, and large clavulate spines only on apical extremity or apical 1/3 of spicule at most (120-150×5-10μm). Subectosomal extra-axial styles absent. Ectosomal auxiliary styles vestigial and scattered within the choanosome (220-275×1-2μm). Microscleres absent.

REMARKS. This species is still known only from a surviving fragment of Schmidt's (1870) holotype, redescribed by Topsent (1920) and reillustrated by Hooper (1991). Although some features of the species are unknown, we do have sufficient details of skeletal structure, spicule morphology and spicule dimensions to clearly distinguish this species from all other raspailiids with rhabdostyle-like echinating spicules. It is particularly characteristic in its rhabdostyle morphology, which more closely resembles those of *Raspaxilla* species than of *Endectyon* species (cf. Hooper, 1991: 1284). Recently Pulitzer-Finali (1994) briefly described a specimen collected from the Kenya region which he assigned to *E. hamatum* (Schmidt). Unfortunately no illustrations were provided (and material from the Genova Museum is not

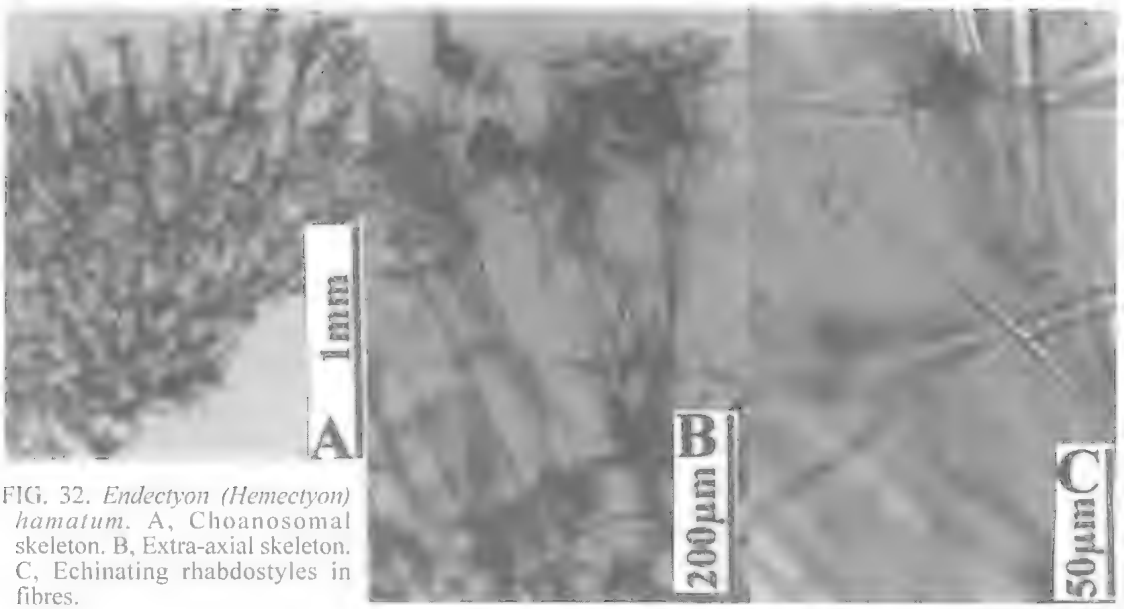



FIG. 32. *Endectyon (Hemectyon) hamatum*. A, Choanosomal skeleton. B, Extra-axial skeleton. C, Echinating rhabdostyles in fibres.

presently accessible for loan). However, it is clear when comparing both descriptions that the E African population is not conspecific with the Caribbean species (i.e. it has long subectosomal extra-axial styles lacking in *E. hamatum*, and several notable differences in spicule dimensions). It is likely that Pulitzer-Finali's (1994) species is new, but its generic placement remains is uncertain.

## DISCUSSION

*Aulospongus* differs from other Raspailiidae in having two size categories of rhabdostyles (the larger, smooth or partially spined rhabdostyles coring fibres, and the smaller, usually spined rhabdostyles echinating fibres); a plumose skeletal structure composed of ascending compressed fibre-bundles (with few or no reticulate elements, and in cases where reticulate interconnecting fibres are present these are usually aspicular and disappear completely in the peripheral skeleton); lacking any differentiation between axial and extra-axial regions of the skeleton (although plumose fibres are slightly more compressed in the axis than in the periphery). Although traditional definitions of the genus are based on possession of a 'peculiar tubular' growth form, exclusively plumose (i.e. non-reticulate) skeletal fibre-bundles, absence of any ectosomal specialisation, and distinctive rhabdose spicules, many species (including the type species *A. tubulatus*), show variations on this supposedly 'typical' theme, such that the previously sharp generic boundary blurs somewhat with other raspailiids which have rhabdose echinating acanthostyles (viz. *Raspailia* (*Raspaxilla*), and to a lesser extent *Endectyon* (*Hemectyon*)). Detailed comparisons between these genera are discussed below, and the range of characters and character states are listed in Table 3.

ANALYSIS OF CHARACTERS. *Growth form.* The characteristic 'tubular' growth form seen in the type and several other species of *Aulospongus* (whereby large fibres are fused together into bundles to form a massive tubular construction), is supposedly 'typical' of the genus and is certainly unusual amongst Raspailiidae. This feature, however, is not universal amongst all *Aulospongus*, with a great variety of growth forms amongst species. Growth forms range from: arborescent, with cylindrical branches seen in many raspailiids including *Raspailia*, *Raspaxilla*, *Hemectyon* and *Thrinacophora*; cylindrical club-shaped with bulbous surface processes seen in *A. samariensis* sp. nov.; massive, subspherical, bushy in *A. villosa*; 'typical' *Aulospongus* form of subspherical, massive, tubular in *A. tubulatus*; plate-like, vasiform in *A. flabellum* and *A. involutum*; bulbous-lobate, thickly lamellate in *A. cerebella*, *A. gardineri* and *A. novaecaledoniensis* sp. nov.; and bulbous encrusting in *A. monticularis* and *A. spinosum* (Table 3).

Determination of whether particular growth forms are derived or ancestral is relatively subjective and equivocal in any character analysis (e.g. Hooper, 1991), but there is already some precedence for such interpretations amongst several groups of demosponges: Axinellidae (Alvarez & Crisp, 1994), Rhabderemiidae (van Soest & Hooper, 1993), *Acarnus* (van Soest et al., 1991), Microcionidae (Hooper, 1996), Mycalidae (Hajdu, in press). Based on outgroup analyses these studies hypothesise that the more massive, erect growth forms are less derived than thinly encrusting ones, the latter frequently indicative of successful adaptation and survival in ephemeral habits, such as the intertidal zone and interstitial habitats. Amongst Raspailiidae 'typical' growth forms are erect, digitate, branching sponges, with far fewer encrusting or bulbous species, and this interpretation is consistent for *Aulospongus*, which is interpreted here as being a highly derived raspailiid. However, this interpretation must be taken with caution because it is likely that species independently colonise these ephemeral habitats, and more unlikely that they have evolved there.

*Plumose fibre bundles.* Species of *Aulospongus* are characterised in having their fibres and spicule tracts amalgamated into bundles, termed here 'fibre-bundles', composed of bulbous spongin fibres cored and echinated by rhabdostyles in plumose tracts, forming individual plumose ascending (usually non-reticulate) branches, and terminating as surface lobes and/or processes. This feature is apparently unrelated to overall growth form and also appears to be unique within Raspailidae. These fibre-bundles are superficially reminiscent of the spiculo-spongin tracts seen in *Pseudaxinella* (Axinellidae) (see Hooper & Lévi, 1993) and *Clathria* (*Microciona*) (Microcionidae) (see Hooper, 1996), although fibre structure and localisation of spicules associated with these fibres are substantially different in both these genera, and there is no inferred relationship between them and *Aulospongus*. Similarly, in *R.* (*Raspaxilla*) *phakellina*, and some other species assigned to *Raspaxilla*, ascending fibres are plumose and dominate the extra-axial skeleton, with (e.g. *R.* (*R.*) *reticulata*) or without (e.g. *R.* (*R.*) *compressa*), interconnecting fibres extending all the way to the peripheral skeleton. However, in these species fibres are generally not bulbous, nor do spicules form dense plumose tracts around the bulbs, amalgamated at the core but diverging towards the periphery, as in *Aulospongus*. Instead, fibres in *Raspaxilla* arise from a well developed, compressed reticulate axis, connecting fibres are paucispicular, and skeletal structure can best be described as plumoreticulate. 'Fibre-bundles' are also absent from *Endectyon*.

*Choanosomal skeletal structure.* In *Aulospongus* there is no appreciable difference between the axial or basal region and the peripheral (extra-axial) regions of the skeleton, although there is often a greater degree of amalgamation (or fusion) of the system of plumose fibre-bundles at the core of the skeleton (or base of the sponge), than in the peripheral skeleton (where fibres simply diverge further apart). Reticulate fibres are present in the axial skeletons of several species (*A. tubulatus*, *A. gardineri*, *A. spinosum*, *A. novaecaledoniensis* sp. nov., *A. samariensis* sp. nov.), in which there are few aspicular or rarely paucispicular (transverse) fibres interconnecting adjacent (ascending) plumose fibre-bundles, but these do not persist into the peripheral region and cannot be classed as 'reticulate' skeletons.

By comparison, *Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*) have well differentiated axial and extra-axial skeletons; well developed, compressed, reticulate axial skeletons; and plumoreticulate or radial extra-axial skeletons (similar to most other raspailiids). In these genera extra-axial skeletal structure consists of plumose ascending multispicular fibres interconnected by uni- or paucispicular transverse fibres that persist all the way to the surface. In some of these species where axial compression is extreme, or where the diameter of the skeleton is narrow (e.g. thin branches), extra-axial tracts are reduced to single radial subectosomal extra-axial styles embedded in and perpendicular to the axis, protruding through the surface, with echinating rhabdostyles appearing to be 'pushed' to the outer edge of the skeleton.

In choanosomal skeletal structure species of *Aulospongus* fall into two groups, with two other character states seen in the Raspailiidae outgroups (*Raspailia* (*Raspailia*), *Raspailia* (*Raspaxilla*), *Endectyon* (*Hemectyon*), *Thrinacophora*). Skeletal structures include: species with compressed axial and radial extra-axial skeletons (the latter composed of subectosomal extra-axial styles embedded in and perpendicular to the axial skeleton), seen in many raspailiids including *Endectyon* (*Hemectyon*) and *Thrinacophora* (this is probably a reduced,

TABLE 3. List of characters and character states used to judge apomorphy in the construction of the cladogram of relationships between species of *Aulospongus* based on outgroup comparisons with members of the family Raspailiidae.

**1.** Growth form: **1(1)**, arborescent, cylindrical branches; **1(2)**, cylindrical club-shaped with bulbous surface processes; **1(3)**, massive, subspherical, bushy; **1(4)**, subspherical, massive, tubular, erect digitate cup-shaped; **1(5)**, plate-like, vasiform; **1(6)**, bulbous-lobate; **1(7)**, bulbous encrusting. **2.** Fibre-bundles: **2(1)**, absent; **2(2)**, present. **3.** Axial skeleton: **3(1)**, compressed, solid; **3(2)**, compressed, more open-reticulate; **3(3)**, slightly compressed, predominantly plumose, few reticulate connections; **3(4)**, exclusively plumose, slightly compressed, no fibre reticulation. **4.** Extra-axial skeleton: **4(1)**, radial, with longer extra-axial auxiliary styles/ anisoxeas embedded in and perpendicular to axis, with or without unispicular reticulate connections; **4(2)**, reticulate or slightly plumoreticulate, reticulate connections persistent throughout; **4(3)**, plumose, few aspicular or unispicular reticulate connections disappearing in periphery; **4(4)**, exlusively plumose, without reticulate connections. **5.** Location of protruding extra-axial styles/ anisoxeas: **5(1)**, absent; **5(2)**, embedded in ascending peripheral fibres and protruding through surface, singly or in bundles. **6.** Interconnecting reticulate fibres: **6(1)**, well developed, persistent throughout skeleton; **6(2)**, well developed in axis, poorly developed in extra-axial skeleton; **6(3)**, vestigial, with aspicular or unispicular interconnecting fibres diminishing along ascending fibres and absent from periphery; **6(4)**, absent completely. **7.** Location of (smaller) echinating styles or rhabdostyles: **7(1)**, evenly dispersed throughout skeleton; **7(2)**, restricted to axis, absent from periphery; **7(3)**, reduced in axis, concentrated mainly in peripheral skeleton embedded in primary ascending fibres, protruding through surface; **7(4)**, localised to outer surface of peripheral fibres, echinating surface and/or forming brushes around protruding extra-axial auxiliary spicules; **7(5)**, absent (presumed secondary loss). **8.** Specialised 'raspailiid ectosomal skeleton': **8(1)**, well developed, composed of brushes of ectosomal auxiliary styles/ anisoxeas surrounding the longer protruding subectosomal extra-axial styles; **8(2)**, vestigial, composed of sparse ectosomal auxiliary styles/ anisoxeas scattered on or below the surface, not forming bundles, with or without the longer protruding subectosomal extra-axial styles; **8(3)**, vestigial, with only protruding long subectosomal extra-axial styles but no ectosomal auxiliary styles; **8(4)**, absent, lacking any ectosomal or extra-axial auxiliary spicules. **9.** Basal rhabds on styles: **9(1)**, absent (never present); **9(2)**, present only on echinating styles/ acanthostyles; **9(3)**, present on both echinating and principal styles/ acanthostyles, **9(4)**, absent (secondarily modified). **10.** Spination on rhabdostyles: **10(1)**, rhabdose spicules absent completely; **10(2)**, smaller echinating acanthostyles spined or partially spined, and at least partially rhabdose, whereas larger choanosomal principal styles entirely smooth and non-rhabdose; **10(3)**, larger choanosomal principal rhabdostyles entirely smooth, echinating rhabdostyles spined or partially spined, basal rhabd moderate or slightly developed on both sorts of spicule; **10(4)** both echinating and choanosomal principal rhabdostyles at least partially spined, basal rhabd strongly developed on both. **11.** Number of categories of (smaller) echinating rhabdostyles: **11(1)**, none; **11(2)**, one; **11(3)**, two. **12.** Raphide microscleres: **12(1)**, present; **12(2)**, absent.

derived character related to the degree of axial compression and loss of a more extensive extra-axial skeleton); species with a compressed reticulate axis, and a reticulate or plumo-reticulate extra-axis in which interconnecting fibres persist throughout the entire peripheral skeleton, also seen in many raspailiids including *Raspailia* (*Raspaxilla*) and *R.* (*Raspailia*); species with few aspicular or occasionally paucispicular fibres interconnecting the ascending plumose fibre-bundles, with reticulate connecting fibres diminishing and disappearing towards the periphery, seen in *A. gardineri*, *A. spinosum*, *A. tubulatus*, *A. novaecaledoniensis* sp. nov. and *A. samariensis* sp. nov.; species with exclusively plumose fibre-bundles arising from a slightly compressed base, with fibres diverging towards the periphery, without any reticulate connections, seen in *A. cerebella*, *A. involutum*, *A. monticularis* and *A. villosa*. These skeletal structures are subdivided into several characters, based on the subdivision of the skeleton into axial, extra-axial and peripheral skeletons, and the presence, absence and nature of reticulate skeletal tracts (Table 3).

In *Aulospongus* there appears to be a correlation between possession of massive, encrusting or tubular growth forms and absence of any notable axial compression, versus possession of lamellate or branching, flexible growth forms with a compressed axial skeleton. Presumably this is an ecological response to a flexible growth form (and consequently of debatable phylogenetic significance). In all these species the ascending plumose fibre-bundles dominate the skeleton and this is a major feature of *Aulospongus*.

*Ectosomal specialisation*. *Aulospongus* was originally described without a specialised 'raspailiid ectosomal skeleton' (i.e. with brushes of ectosomal auxiliary styles/anisoxeas surrounding the longer protruding subectosomal extra-axial styles), and lacking any ectosomal auxiliary and subectosomal extra-axial spicules. These characters were also overlooked in the recent review of Raspailiidae (Hooper, 1991). More detailed re-examination of type material, however, confirms there is a gradual transition-series amongst species in 'raspailiid ectosomal structure', falling into four groups: 1) well developed (seen in *A. gardineri* and *A. samariensis* sp. nov.); 2) vestigial, with sparse ectosomal auxiliary styles/anisoxeas scattered on or below the surface, not forming bundles, with or without the longer protruding subectosomal extra-axial styles (in *A. novaecaledoniensis* sp. nov., *A. involutum* and *A. tubulatus*); 3) vestigial, with only protruding long subectosomal extra-axial styles but no ectosomal auxiliary styles (seen in *A. monticularis*); 4) and absent completely, without any ectosomal or extra-axial auxiliary spicules (in *A. cerebella*, *A. flabellum*, *A. spinosum* and *A. villosa*) (Table 3).

The possession of a well developed ectosomal skeleton is interpreted here as a primitive condition and the retention of an ancestral (family) characteristic, but probably more importantly, it also appears to be an unstable character even within genus-groups. For example, *Raspailia (Raspailia) wilkinsoni* Hooper lacks specialised ectosomal spicules, with only choanosomal and extra-axial spicules protruding (corresponding to group 3 above); *R. (R.) echinata* Whitelegge has long protruding extra-axial styles with very few vestigial ectosomal styles embedded on the surface but not forming characteristic raspailiid surface brushes (group 2); whereas most raspailiids, such as *R. (R.) vestigifera* Dendy and *R. phakellina* Topsent, have well developed 'raspailiid ectosomal skeletons' (group 1 above). *Endectyon* (*Hemectyon*) has vestigial ectosomal auxiliary spicules scattered within the choanosome (but not forming surface brushes) (group 2 above), whereas its senior generic synonym *Endectyon* retains the specialised 'raspailiid ectosomal skeleton' (group 1 above) (Hooper, 1991).

Under this interpretation, *Aulospongus* group 1 species, with well developed 'raspailiid ectosomal skeletons', are more primitive (ancestral) than others; vestigial ectosomal skeletons (groups 2-3) are more derived, representing a gradual secondary loss of this character; and group 4 species that have completely lost any ectosomal skeletal specialisation are most derived. A similar interpretation was taken for the raspailiid genus *Echinodictyum* by Hooper (1991), in which only one of thirteen Australian species possessed a 'typical raspailiid ectosomal skeleton', the others likely to have secondarily lost these spicules completely.

*Rhabdose spicules*. The most significant character shared by *Aulospongus*, *Raspaxilla* and to a lesser degree *Hemectyon* is the possession of echinating rhabdostyles. The existence of this character in other demosponge families suggests they are homoplasic developments, whereas within the group *Aulospongus* - *Raspaxilla* the smaller echinating rhabdostyles are clearly homologous derivatives of typical echinating acanthostyles, and for *Aulospongus* the possession of these spicules is synplesiomorphic. Conversely, the larger choanosomal principal rhabdostyles found only in *Aulospongus* are unique and synapomorphic.

Generally, the coring and echinating rhabdostyles of *Aulospongus* are much more similar in their morphology, including the possession of spines on the larger choanosomal principal spicules, whereas in *Raspailia* (*Raspaxilla*), *Endectyon* (*Hemectyon*) and other raspailiids coring spicules are non-rhabdose, entirely smooth, with distinctly different geometry than echinating spicules. In *Aulospongus* there are two groups of species with different patterns of spination on rhabdostyles: one group with larger choanosomal principal rhabdostyles entirely smooth, echinating rhabdostyles spined or partially spined, basal rhabd moderate or slightly developed on both sorts of spicules (seen in *A. cerebella*, *A. flabellum*, *A. monticularis*, *A. spinosum*, *A. tubulatus*); and the other group with both echinating and choanosomal principal rhabdostyles at least partially spined, basal rhabd strongly developed on both (in *A. gardineri*, *A.*

TABLE 4. Taxon-character matrix for *Aulospongus* and outgroups *Raspailia* (*Raspaxilla*), *Raspailia* (*Raspailia*), *Endectyon* (*Hemectyon*) and *Thrinacophora* (*=type species). See Table 3 for explanation of characters and their states. Consistency index (C.I.) and Rescaled Retention Index (R.C.) is indicated for each character obtained from parsimony analysis (Swofford, 1993).

| Species | Character | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| *A. cerebella* | 6 | 2 | 4 | 4 | 1 | 4 | 1 | 4 | 3 | 3 | 2 | 2 |
| *A. flabellum* | 5 | ? | ? | ? | 1 | ? | ? | 4 | 3 | 3 | 2 | 2 |
| *A. gardineri* | 6 | 2 | 3 | 3 | 2 | 3 | 1 | 1 | 3 | 4 | 3 | 2 |
| *A. involutum* | 5 | 2 | 4 | 4 | 2 | 4 | 1 | 2 | 3 | 4 | 2 | 2 |
| *A. monticularis* | 7 | 2 | 4 | 4 | 2 | 4 | 1 | 3 | 3 | 3 | 2 | 2 |
| *A.novaecaledoniensis* | 6 | 2 | 3 | 3 | 1 | 3 | 2 | 2 | 3 | 4 | 2 | 2 |
| *A. samariensis* | 2 | 2 | 3 | 3 | 2 | 3 | 1 | 1 | 3 | 4 | 2 | 2 |
| *A. spinosum* | 7 | 2 | 3 | 4 | 1 | 3 | 1 | 4 | 3 | 3 | 3 | 1 |
| *A. tubulatus** | 4 | 2 | 4 | 4 | 1 | 4 | 1 | 2 | 3 | 3 | 2 | 2 |
| *A. villosa* | 3 | 2 | 4 | 4 | 1 | 4 | 1 | 4 | 3 | 4 | 2 | 2 |
| *R. (R.) phakellina** | 1 | 1 | 2 | 2 | 2 | 2 | 3 | 1 | 2 | 2 | 2 | 2 |
| *R. (R.) typica** | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 |
| *E. (H.) hamatum** | 1 | 1 | 1 | 1 | 1 | 2 | 4 | 2 | 2 | 2 | 2 | 2 |
| *T. funiformis** | 1 | 1 | 1 | 1 | 2 | 2 | 5 | 1 | 1 | 1 | 1 | 1 |
| C.I. | 0.86 | 1.00 | 0.75 | 0.75 | 0.33 | 1.00 | 1.00 | 0.60 | 1.00 | 0.60 | 0.67 | 0.50 |
| R.C. | 0.64 | 1.00 | 0.66 | 0.67 | 0.22 | 1.00 | 0 | 0.40 | 1.0 | 0.40 | 0.33 | 0 |

*involutum*, *A. novaecaledoniensis* sp. nov.; *A. villosa*, *A. samariensis* sp. nov.). Most species of *Aulospongus* have only one category of smaller echinating rhabdostyles, whereas two species have a second category which is slender, entirely smooth, and differentiated from the spined echinating rhabdostyles (*A. gardineri* and *A. spinosum*) (Table 3).

*Microscleres.* Raphide microscleres occur in several raspailiid genera (singly or in trichodragmata): *Aulospongus*, *Thrinacophora*, *Trikentrion* and *Eurypon* (with synonyms *Tricheurypon* and *Protoraspailia*), and *Rhadbeurypon.* Thus, the presence of raphides in one species of *Aulospongus* (*A. spinosum*), is interpreted here to represent the retention of an ancestral family character (following Hooper, 1991), with the corollary that loss of raphides is a secondarily derived character given that it is more parsimonious that these spicules are independently lost than independently acquired.

PHYLOGENETIC ANALYSIS. Table 4 shows the distribution of characters and character-states amongst species of *Aulospongus* and the raspailiid outgroups. Several outgroups were chosen representing a range of affinities with *Aulospongus*, their characters described from the type species of each taxon as follows: *Raspailia* (*Raspaxilla*) (type species *Raspaxilla phakellina* Topsent, holotype fragment MNHN LBIM DT1614); *R.* (*Raspailia*) (type species *R. typica* Nardo, holotype lost, Schmidt's 'representative specimen' from the Adriatic BMNH 1867.3.11.8), *Endectyon* (*Hemectyon*) (type species *Raspailia ? hamata* Schmidt, holotype fragment MNHN LBIM DT2161); and *Thrinacophora* (type species *T. funiformis* Ridley & Dendy, holotype BMNH 1887.5.2.53).

Phylogenetic analysis found good statistical support for the differentiation of *Aulospongus* from both closely related (*Raspaxillla*, *Raspailia*) and more distantly related raspailiid outgroups (*Endectyon*, *Thrinacophora*) (Bootstrap/Decay indices = 93/3; Fig. 33). Principal differentiating characters for *Aulospongus* consist of the synapomorphies: possession of plumose fibre-bundles (character 2); both principal and echinating styles with rhabdose bases, and patterns of spination on rhabdostyles (characters 9-10); and a synplesiomorphy of echinating rhabdostyles more-or-less evenly distributed throughout the skeleton, not confined to the peripheral skeleton (character 7) (Fig. 33; length = 43; number of minimum length trees = 36; consistency index = 0.744; retention index = 0.796; rescaled retention index = 0.593). Characters 5 (location of protruding extra-axial spicules), 7 (location of echinating styles/ rhabdostyles), 11 (number of

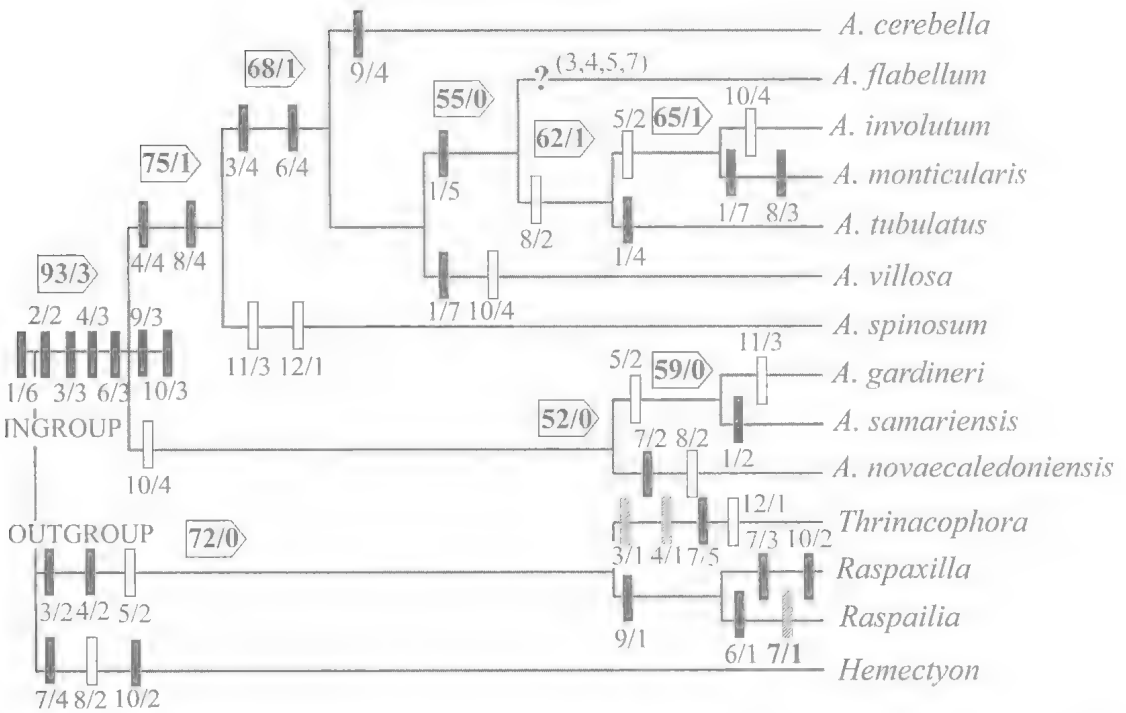



FIG. 33. Phylogenetic analysis of *Aulospongus* using parsimony (Paup 3.1.1), indicating the most parsimonious tree (of 36 possible minimum length trees), with characters 3, 4 and 6 ordered (Table 4). Character state changes, under accelerated transformation (ACCTRAN), are indicated as character/state; solid bars = synapomorphies; open bars = parallelisms; stippled bars = reversals. Statistical support for branching, indicated inside the arrows at branch nodes, as bootstrap/decay values.

categories of echinating rhabdostyles) and 12 (possession of raphides) were the least informative, with rescaled retention index ranging from 0-0.33 (Table 4).

The high numbers of homoplasic character states and relatively low bootstrap/decay indices supporting branching suggest that the phylogeny of the genus is not fully resolved by this analysis. However, within *Aulospongus* two groups of species are clearly indicated (Fig. 33), differentiated mainly by their choanosomal skeletal structures (ordered characters 3,4,6), with moderate level of statistical support (Bootstrap/Decay = 75/1). Group 1 species (*A. cerebella*, *A. involutum*, *A. monticularis*, *A. tubulatus*, *A. villosa*, and *A. spinosum*) have a plumose axial skeleton composed of compressed, 'fused' fibre-bundles, axial and extra-axial skeletons with exclusively plumose structure, lacking any interconnecting reticulate tracts in the peripheral skeleton. *Aulospongus flabellum* is tentatively included in this group, despite the unknown status of these characters (i.e. not described by Pulitzer-Finali, 1994), based on inferred closer similarities with other Group 1 species than with Group 2 species in growth form and pattern of spination on rhabdostyles. Group 2 species (*A. gardineri*, *A.samariensis*, *A. novaecaledoniensis*) have vestigial reticulate fibres remaining in the extra-axial skeleton, although these diminish as they ascend towards the periphery and disappear altogether in the outer skeleton. By comparision, the raspailiid outgroups have reticulate fibres persistent throughout the axial and extra-axial skeletons.

All Group 2 species have spines on both larger (choanosomal) and smaller (echinating) rhabdostyles (character 10/4) (*A. gardineri, A. samariensis*, *A. novaecaledoniensis*), but this feature is also present in two Group 1 species (*A. villosa, A. involutum*), whereas all other Group 2 species have completely smooth choanosomal principal rhabdostyles (character 10/3; *A. cerebella, A. flabellum, A. monticularis, A. tubulatus, A. spinosum*). This is interpreted as a homoplasic development, given that none of the



FIG. 34. Geographic distribution of *Aulospongus* species. Group 1 species (1, *A. cerebella*, 2, *A. monticularis*, 3, *A. spinosum*, 4, *A. tubulatus*, 5, *A. involutum*, 6, *A. villosa*, 7, *A. flabellum*); group 2 species (A, *A. gardineri*, B, *A. samariensis* sp. nov., C, *A. novaecaledoniensis* sp. nov.).

outgroup taxa have spined principal choanosomal spicules. However, it is also possible that character 10/4 is synplesiomorphic for *Aulospongus*, with the more derived state (10/3) occurring through secondary loss of spines on principal rhabdostyles.

The possession, loss and modification of a 'raspailiid ectosomal skeleton' (character 8) is also clearly homoplasic within *Aulospongus*. This supports the view of Hooper (1991) that the independent secondary loss (derivation) of ectosomal specialisation occurs in virtually all raspailiid genera, even though it is supposedly a major synapomorphy for Raspaillidae. In *Aulospongus* several species retain (the ancestral) specialised condition (*A. gardineri*, *A. samariensis*), others have no specialised ectosomal skeleton at all (*A. cerebella*, *A. flabellum*, *A. spinosum*, *A. villosa*), and others have conditions intermediate to these, with partial loss of spicules types and/or ectosomal skeletal structures (*A. involutum*, *A. monticularis*, *A. novaecaledoniensis*, *A. tubulatus*). Thus, ectosomal skeletal structure is the most easily



FIG. 35. Geographic distribution of *Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*) species. A. *R.*(*R.*) *acanthifera*, B. *R.*(*R.*) *clathrioides*, C, *R.*(*R.*) *compressa*, D, *R.*(*R.*) *flaccida*, E, *R.*(*R.*) *folium*, F, *R.*(*R.*) *frondula*, G. *R.*(*R.*) *galapagensis*, H, *R.*(*R.*) *hirsuta*, I, *R.*(*R.*) *hyle*, J, *R.*(*R.*) *hymani*, K, *R.*(*R.*) *inaequalis*, L, *R.*(*R.*) *mariana*, M, *R.*(*R.*) *phakellina*, N, *R.*(*R.*) *reticulata*, O, *R.*(*R.*) *topsenti*, P, *R.*(*R.*) *wardi*, 1, *E.*(*H.*) *hamatum*, 2, '*E. hamatum*' sensu Pulitzer-Finali (1993)).

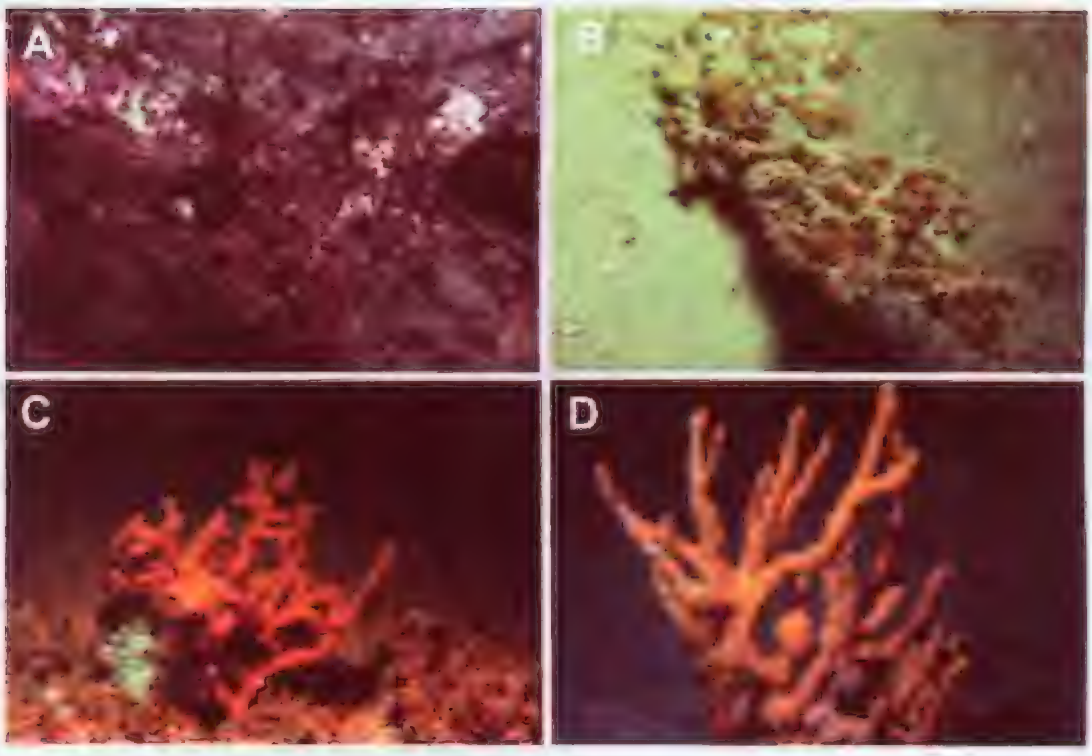



FIG. 36. A, *Aulospongus samariensis* sp. nov. (W Caribbean population), Santa Marta, Colombia (photo S. Zea). B, *Aulospongus samariensis* sp. nov. (E Caribbean population), Discovery Bay, Jamaica (photo H. Lehnert). C, *Raspailia* (*Raspaxilla*) *clathrioides* (Lévi), SW Noumea Lagoon, New Caledonia (photo G. Bargibant). D, *Raspailia (Raspaxilla) reticulata* Hooper, Low Isles, Great Barrier Reef (photo J. Hooper).

modified (or lost) feature within the genus (and family), and consequently the least valuable diagnostic character amongst *Aulospongus*.

BIOGEOGRAPHY. The distribution of *Aulospongus* (Fig. 34) is pan-equatorial, predominantly tropical – subtropical, with rare incursions into cooler temperate waters. The central E Atlantic region contains two species, both from Group 1 (*A. monticularis*, *A. spinosum*, the latter with incursion into the Mediterranean Sea); the central American (E Pacific) – Caribbean (W Atlantic) region contains two species, with representatives from both Groups 1 and 2 (*A. cerebella*, *A. samariensis*, respectively); the W Pacific region contains only two species from both Groups 1 and 2 (*A. villosa*, *A. novaecaledoniensis*, respectively); and the W Indian Ocean region contains four species, also with representatives from both groups 1 and 2 (*A. tubulatus*, *A. involutum*, *A. flabellum* and *A. gardineri*, respectively). To date no species have been recorded for the Indo-Malay archipelago, Australasia or the Pacific islands apart from a deeper water record from New Caledonia.

Distribution of *Raspaxilla* is different to that of *Aulospongus* (Fig. 35). *Raspaxilla* species are virtually centred on the Pacific rim, distributed in tropical, temperate and antiboreal waters, extending into the subantarctic islands and Antarctica peninsula. To date there are no records of *Raspaxilla* species from either the Atlantic or Indian Oceans. Similarly, *Hemectyon* is so far known only from the type species in the Caribbean. The species and genus allocation of Pulitzer-Finali's (1994) specimen from the W Indian Ocean (Fig. 32, number 2), is presently unknown, but clearly not conspecific to *E.* (*H.*) *hamatum*.

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**STATUS OF *PARAPLAGUSIA NOTATA* (DE VIS, 1883).** *Memoirs of the Queensland Museum 43(2): 708. 1999:-* The appropriate designation for *Plagusia (=Paraplagusia) notata* De Vis, 1883 is uncertain because of an apparently insoluble problem with 2 putative holotypes from Moreton Bay. The first, QMI107, was both registered and labelled as 'type' in 1911 by Ogilby, who was appointed Queensland Museum Curator of Fishes the following year. The second, AMSI379, is identified as the holotype of *Plagusia notata* by Menon (1979). He had the specimen examined (by Dr P. Whitehead) at the British Museum and considered it to be a junior synonym of *Paraplagusia bilineata*. Australian Museum records indicate that this specimen was obtained on exchange from the QM in 1886 but do not refer to its type status. The type status of these 2 specimens cannot be ascertained conclusively from the type description (De Vis, 1883) and was not resolved by Eschmeyer (1998) in his treatment of the species. De Vis is notorious for imprecision (Ingram, 1990) and this continues to account for confusion about the status of many of his nominal species. The 2 specimens are not conspecific. QMI107 is identifiable as *P. sinerama* Chapleau & Renaud, 1993. The specimen is damaged posteriorly, precluding accurate fin ray and vertebral counts, but has short unbranched labial papillae and 3 lateral lines on the ocular side. The combination of these characters distinguish *P. sinerama* from all other known species of the genus *Paraplagusia* (see Chapleau & Renaud, 1993). Although this suggests that *P. notata* may be a senior synonym of *P. sinerama*, De Vis' description of the colour pattern of *P. notata* as including 'black lines enclosing pale angular spots' is inconsistent with *P. sinerama* which is uniformly dark brown on the ocular side. If the original description is correct, it is doubtful that QMI107 is the holotype and it is probable that Ogilby mislabelled this specimen. AMSI379 cannot be located in the collections of the Australian Museum (M. McGrouther pers. comm., 1997). Menon's identification of it as *P. bilineata*, a species possessing pale spots on the ocular side, corresponds with De Vis' description of the colouration of *P. notata*. It is therefore likely that *P. notata* is either a junior synonym of *P. bilineata* or an available name for an unidentified species of *Paraplagusia*. On this basis, QMI107 and seven other specimen lots in the Queensland Museum from Moreton Bay are identified as *P. sinerama*, a species previously recorded only from NW Australia. Johnson (1999) also records *P. bilineata* and an unidentified species of *Paraplagusia* from the type locality.

**Acknowledgements**

Dianne Bray and Mark McGrouther kindly assisted with checks of the Australian Museum Collection. Martin Gomon (Museum Victoria) provided helpful comments on the manuscript.

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# ANNOTATED CHECKLIST OF THE FISHES OF MORETON BAY, QUEENSLAND, AUSTRALIA

Johnson, J.W. 1999 06 30: Annotated checklist of the fishes of Moreton Bay, Queensland, Australia. *Memoirs of the Queensland Museum* **43**(2): 709-762. Brisbane. ISSN 0079-8835.

J.W. JOHNSON

A total of 750 species of marine and estuarine fishes are recorded from Moreton Bay, Queensland, Australia. Of the species recorded, 355 are considered uncommon or rare, 132 are at the southern limit and 26 are at the northern limit of their known distribution on the east coast of Australia. Many species reported represent significant extensions of their known range. ❐ *Checklist, fishes, biodiversity, Moreton Bay, Queensland, Australia.*

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Moreton Bay is a large, broadly triangular, semi-enclosed, subtropical bay and tidal estuary. A total of 750 species of marine and estuarine fishes are recorded from the area. High species diversity in fishes is often associated with large diverse coral reefs, a feature absent from this area. The extent of coral growth is restricted to several small localised reefs and fringing reef off a few low wooded islands. In Moreton Bay, relatively high diversity appears to be a function of a wide array of habitat types and a crossover between the ranges of tropical and temperate species. Moreton Bay has been highly productive, yielding a significant proportion of the commercial and recreational catch of Queensland despite exploitation of the fishery for over a century. Of the species recorded, 355 are considered uncommon or rare, 132 are at the southern limit and 26 are at the northern limit of their known distribution on the east coast of Australia. The large proportion of uncommon and rare species may be due to the long period over which fishes have been collected increasing the chances of occasional records of rare, extralimital, vagrant deep water and oceanic species and the dynamic and marginal nature of some major habitat types. Many species records reported represent significant extensions of known range.

## GEOGRAPHY AND HYDROLOGY

Moreton Bay covers an area of approximately 1600km2 between Comboyuro Pt (27°04'S) and the Nerang River mouth (27°59'S). It is bounded by the mainland of the greater Brisbane region to the west and by two large sand islands, Moreton and Stradbroke, to the east. Connection to the ocean is via four separate entrances, by far the largest of which is a 15km wide complex system of channels and sand banks between Bribie and Moreton Islands. Narrower entrances are found at South Passage, Jumpinpin and the recently stabilised Southport seaway. The width of the bay varies from 1 to 33km, with the southern section narrowing into mangrove islands and river delta. The northern and eastern shores of Moreton Bay differ generally from those of the west and south through higher salinity, narrower temperature range, lower turbidity, more coarse sand and greater diversity of seagrass species.

Numerous creeks and rivers discharge into the bay, the most significant of which is the Brisbane River followed by the North and South Pine, Logan, Nerang, Coomera and Caboolture Rivers. Reviews of the physical and biological environment of the Brisbane R. and Moreton Bay catchment are available in Davie et al. (1990) and Tibbetts et al. (1998). The Brisbane R. has a major influence on turbidity and suspended sediment concentration in the bay due to the large sediment load carried during flood. The western area of the bay is characterised by fluctuating salinity and turbidity and reduced floral diversity resulting from the effects of river outflow. Sediment deposited in Moreton Bay consists of river sands and mud, primarily from the Brisbane R. and marine sand transported north by the prevailing north long shore currents of the east coast of Australia. Maxwell (1970) gives a sedimentary framework while Stephens (1992) describes the historic deposition patterns of sediments within Moreton Bay and current deposition zones. The middle of the bay, between the river delta and prodelta to the west and the sandy tidal deltas to the east and north-east, is

essentially a non-depositional area with virtually no sediment cover.

There is very limited potential for the penetration of swell from the Pacific Ocean due to sheltering by Moreton and Stradbroke Is. Prevailing winds are from the south-east, however west to south-west winds are common during winter and north-east winds predominate on summer afternoons. Wind speed rarely exceeds 40 kph. Wave heights build rapidly according to wind strength but also drop quickly as winds abate. An outline of tidal current patterns has been undertaken by Patterson & Witt (1992). Tidal range inside the bay is more than 20 percent greater than that in areas of close proximity outside. Tides are semi-diurnal with a range of 1.8m at mean high water neap to a mean high water spring of 2.2m at the Brisbane bar. Highest annual tides in Moreton Bay rarely exceed 2.7m (Australian National Tide Tables, 1999). Maximum water depth has been recorded on admiralty charts to 44m at low water datum in very localised holes. However, the depth of these holes appear to vary over time and recent soundings were no greater than 34m. Depths along the east channel are largely from 20 to 28m while in the central part of the bay depths from 10 to 15m are prevalent. The bay begins to narrow markedly to the south of Peel Island and the bathymetric profile consists generally of broad shallow tidal banks interposed by a series of steeply shelving channels of 10 to 25m with very isolated holes in excess of 30m.

## CLIMATE AND HABITAT

Long term diurnal ambient temperature ranges (minimum/maximum) average between 20.9 and 29.9°C in January/February and between 9.4 and 20.6°C in July at Brisbane airport (27°25'S 153°05'E). At Cape Moreton (27°02'S 153°28'E) these ranges are narrower, varying from 21.9 to 26.6°C in January/February and 12.9 to 18.7°C in July. Average sea surface temperatures in Moreton Bay range from 16°C in winter to 26°C in summer. As with ambient readings, sea temperatures immediately outside the bay fluctuate less and have a considerably more restricted range. Average annual rainfall figures are 1,213mm at Brisbane airport and 1,566mm at Cape Moreton, with the highest and lowest monthly totals during February/March and September, respectively (Anon., 1988). Salinity is greatly affected by localised freshwater runoff from estuaries, but in areas subject to oceanic influence, it remains relatively stable at about 35ppt.

The main habitats of fishes in Moreton Bay involve mangroves, seagrass meadows, littoral red laterite reef, littoral and sublittoral sandstone reef, subtidal mudstone ledges, shelly algal and sponge beds, fringing coral reef and various grades of generally bare sandy to muddy substrates. The latter substrate types broadly include fine mud, silty sand, shelly sand and clean marine sand (Maxwell, 1970). They occur extensively throughout the bay subtidally and as flats littorally. Man-made structures such as basalt rock breakwaters and retaining walls, as well as artificial reefs constructed of ships, barges, cars and tyres, have attracted species in abundance to sites where they were previously poorly represented or absent (Wright, 1990). As important refugia, they must now be included among the major habitat types. The Southport seaway includes rock breakwaters that are exposed to limited incursion of ocean swell and the only high energy surf areas inside Moreton Bay. A review of fisheries habitats throughout Queensland is available in Zeller (1998).

In the saltmarsh and claypan areas of Moreton Bay and the upper tidal inlets that drain them, fish species diversity is low relative to adjacent mangroves and the abundance of individual species fluctuates widely on a seasonal basis (Morton et al., 1987,1988; Mousalli & Connolly, 1998). Over a 12 month period on Coomera Island only 8 species were recorded from saltmarsh and 19 species of mostly juvenile fishes from an upper drainage inlet. However, these areas are vast, totalling almost 5,000ha throughout Moreton Bay (Hyland & Butler, 1988) and are important feeding grounds for some species (Morton et al., 1987). One gobiid species, *Calamiana* sp., is only known in Moreton Bay from saltmarsh. McLeod (1969) provides a detailed study of the saltmarsh vegetation of Moreton Bay. Approximately 15 percent of high tides inundate these habitats annually. Fishes most commonly found in these areas include gobiids, juvenile mugilids, ambassids and blue-eyes, *Pseudomugil signifer*.

Mangrove forests are prominent in the western and southern areas of Moreton Bay. The region has one of the most highly developed mangrove communities along the Australian east coast in terms of species numbers and structural complexity (Hutchings & Saenger, 1987). Seven mangrove species occur in the area, with

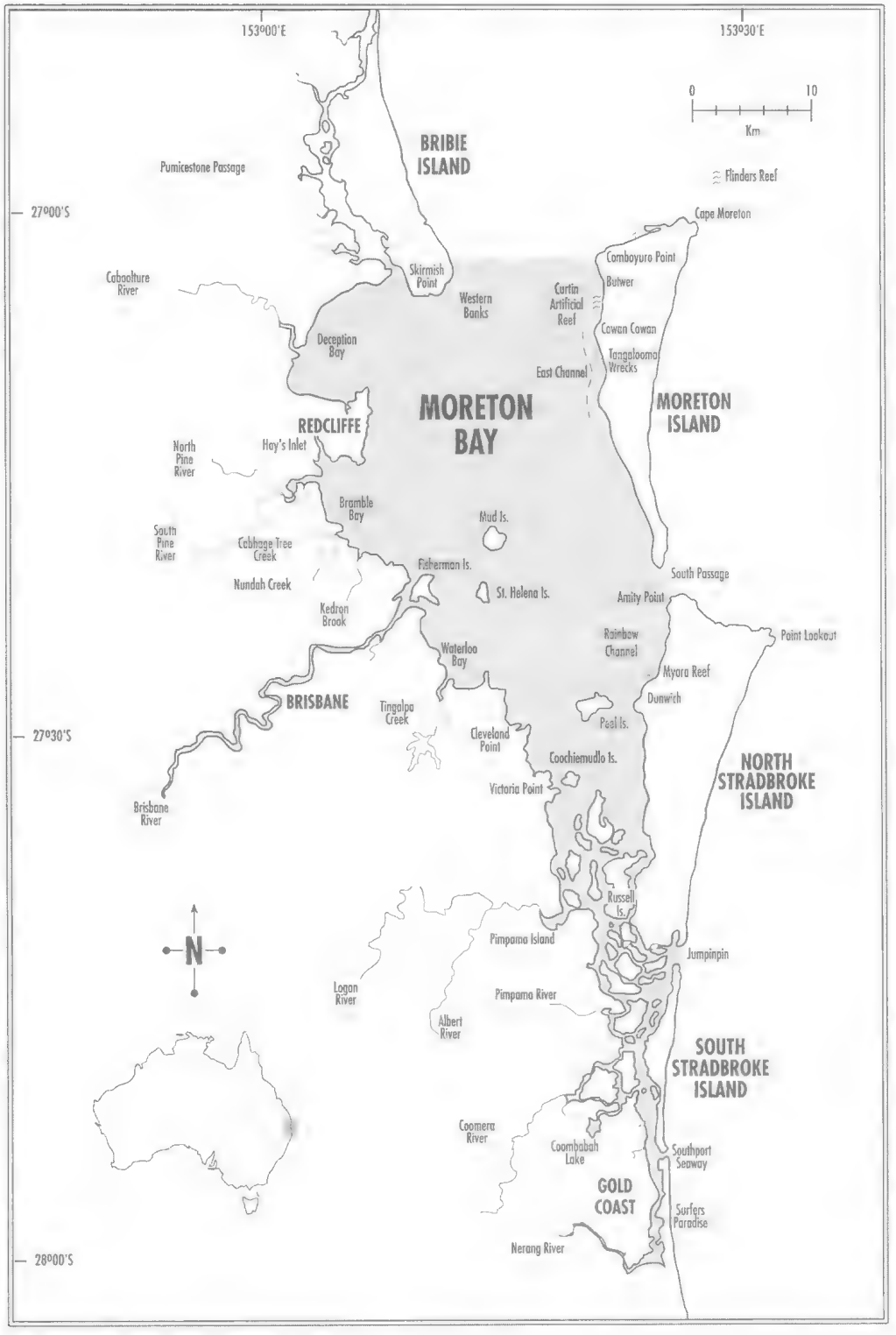



FIG. 1. Moreton Bay region with study area shaded.

*Avicennia marina* dominant (Hyland & Butler, 1988). Williams (1992) estimates that a total of 13,000ha of mangrove forest exist in Moreton Bay, but includes Pumicestone Passage (to Caloundra) in this area. Apart from acting as an important nursery area for juvenile fishes (Morton, 1990; Laegdsgaard & Johnson, 1995), mangroves are a conduit for nutrient inflow to the estuary and adjacent marine environment from the intertidal wetlands (Davie, 1992; Abal et al., 1998). While fishes including engraulids, ambassids, sillaginids, sparids, mugilids and tetraodontids are common in mangrove channels and move among the pneumatophores and prop-roots tidally, some blenniids and gobiids also occur as infauna to the mangrove trees and inhabit small pools and burrows, extending to the supralittoral zone. In examining fish communities in foreshore mangroves at Lota Creek, Moreton Bay, Morton (1990) found that standing crop estimates for fishes among the mangroves were among the highest recorded for an estuarine area in Australia. An analysis of density, biomass and species composition of intertidal mangrove fishes for the near northern Tin Can Bay is given by Halliday & Young (1996).

Seagrass communities of Moreton Bay have been described by Young & Kirkman (1975), Kirkman (1975, 1976) and Abal et al.(1998). Surveys carried out by Hyland et al. (1989) found there were 12,469ha of seagrass meadows and 10,282ha of sparse or patchy seagrass cover in Moreton Bay between the Southport Broadwater and Toorbul Point. Seven species of seagrasses have been recorded, with *Zostera capricorni* predominating. In southern Moreton Bay there is a strong east-west correlation between seagrass depth range and water quality (Abal & Dennison, 1996). Evidence suggests changes in water quality may have caused reductions in seagrass distribution and depth penetration, particularly in the landward part of this area. Seagrass beds are known to vary considerably in extent over time. Extreme flooding in 1974 led to the loss of large areas of seagrass in the Southport broadwater and western Moreton Bay; however by 1980 these areas had largely regenerated (Forbes, 1984). Poiner (1984) evaluated the long term stability of seagrass beds off North Stradbroke I. using aerial photographs. The importance of seagrass and associated epiphytes, microfauna and detritus in providing food and shelter for fishes, prawns and numerous other marine organisms and in stabilising bottom sediments is well known (Poiner et al., 1992; Moriarty et al., 1984; Pollard, 1984). Assemblages of fishes in association with seagrass and bare sand habitat across a wide area of northern New South Wales were sampled, quantified and compared by Gray et al., (1996). In Moreton Bay, hemirhamphids, syngnathids, scorpaenids, teraponids, apogonids, girellids, blenniids, gobiids, siganids, monacanthids and many other fishes are often found in close association with seagrass. Although surveys of the macroalgal communities of Moreton Bay are incomplete, species diversity is high with the area containing at least 275 species, or about 40% of those known from Queensland waters (Phillips, 1998). Little is known of the relationships between fish assemblages and subtropical macroalgae, but the species composition of fish collections from weed beds and adjacent habitats in Moreton Bay indicates that most associations are loose and probably more closely related to the underlying substrate. Several species, including frogfish *Batrachomoeus dubius*, parrotfish *Leptoscarus vaigiensis* and wobbegongs *Orectolobus* spp., were often collected or observed amongst thick algal growth in this area. The predominantly temperate families odacidae, clinidae and gobiesocidae are strongly associated with algae, but are rare in Moreton Bay.

Stands of live coral are now relatively limited and patchy in Moreton Bay, occurring from Mud I. south to Macleay I. and along the mainland coast between Wellington Pt and Point Halloran (Johnson & Neil, 1998). Extensive coraline deposits are present in the substratum however, indicating that coral presence in Moreton Bay today represents a reduction in species diversity and change in dominance from a prior period of greater richness and abundance (Lovell, 1989). Communities were dominated by corals typically associated with low wave action and clear water such as *Acropora*, *Pocillopora* and *Stylophora*. Most modern assemblages, such as those at the northwestern side of Peel I., are dominated by *Favia speciosa* and others of massive form that are more robust and able to tolerate higher levels of sediment cover and lower light penetration. Harrison et al. (1991, 1998) record 42 coral species from Moreton Bay. Myora Reef has the highest diversity (16 species) while Myora and Peel and Goat Is. have the greatest overall coral coverage of reefs in Moreton Bay (Harrison et al., 1998; Johnson & Neil, 1998). The corals of Moreton Bay include species typically associated with tropical, subtropical and temperate waters and could thus be considered to be transitional communities. Clearer oceanic conditions in

adjacent waters support richer more diverse coral communities. Scleractinian coral species to the north number 119 at nearby Flinders Reef (26°59'S), 77 at Mudjimba I. and Gneering Shoals (26°37 - 26°41'S) and 244 on the southern Great Barrier Reef (Veron, 1995; Banks & Harriot, 1995; Harrison et al., 1998). To the south, 90 species have been recorded from the Solitary Islands (29°55' - 30°01'S) (Harriot et al., 1994) and 83 from Lord Howe I. (31°29'-31°36'S) (Harriot, et al., 1995). Lovell (1989) found that of the 25 fringing reefs existing in Moreton Bay before a major flood in 1974, 15 were killed by that flood. After seven years only a single reef had regenerated to a form close to its original composition. The dynamic nature of most coral communities in the bay has undoubtedly been paralleled by an ebb and flow of fish species associated with those corals. The unique, largely monospecific *Acropora digitifera* assemblage at Myora has been mostly unaffected by recent floods, possibly through the input and pooling of oceanic water from the South Passage (Stephenson, 1968; Lovell, 1989) and supports a fish fauna (especially chaetodontids) largely absent from the remainder of Moreton Bay. Rock retaining walls constructed at Amity Point have provided a base for some sparse coral growth previously absent on the current swept sandy substrate and have attracted many species of fishes.

## FISHERIES

Moreton Bay has long been exploited by both recreational and commercial fishers. By the mid 1860's the total commercial fish catch was estimated at 330 tonnes and by 1911 the Brisbane Metropolitan Fish Market had a throughput of about 820 tonnes (Anon., 1997a). During the three years to 1991 the average annual catch marketed was about 1600 tonnes (Quinn, 1992). Unfortunately, long term catch statistics are difficult to compare due to variation in the methods of collection of data (until 1988) and non-inclusion of 'black market' catches, which are reported to have been significant particularly during the 1970's and 1980's (Quinn, 1992). Williams (1992) estimated that about 1000 full time commercial fishers in the Moreton Bay region (including the ocean beaches and adjacent waters) took approximately 10% by value and 16% by weight of the seafood catch of Queensland. About half of this catch was fish. Commercial catches of bream, flathead, mullet, tailor and whiting from Moreton Bay comprise between 35 and 60 percent of the total for Queensland. Although data is limited, recreational catches of all these species, except mullet, are estimated to be comparable with or exceed those of licenced commercial fishers (Quinn, 1992). Otter trawling in Moreton Bay commenced in 1952 and by 1967 about 250 boats were operating at the peak of the season. An early attempt to quantify the catch and catch rates of trawlers in Moreton Bay by Maclean (1973) showed little change between the 1966-67 season and the inception of the fishery. In 1992 Williams found that about 200 trawlers operated in the region, although some for only part of the year. Their catch was estimated at about 41% by weight of the total production for Moreton Bay. Although 85 percent of this landed catch was prawn, large quantities of fish were present in the discarded bycatch. Measures are currently being implemented to encourage the incorporation of bycatch reduction devices into trawl nets, with the intention of reducing the catch of non-target species (both fishes and invertebrates) and preserving their populations. Recent information suggests that the commercial fishery in Moreton Bay is experiencing declines in total catch, stability of catch rates and decreasing numbers of commercial operators. Over the past two decades there has been a significant decline to about 800 commercial operators. With a surrounding human population of over 1.5 million, Moreton Bay makes up less than 3% of the Queensland coastline but absorbs about 30% of the recreational fishing effort and now produces about 13% by weight of Queensland's commercial catch (Anon., 1997a). The activities of about 15 currently licensed aquarium fish collectors operating within the bay are largely centred around the fringing coral reefs of Peel, Bird and Goat Islands, Myora and scattered reefs along the edge of the Rainbow Channel between Dunwich and Amity Point.

## ENVIRONMENTAL CHANGES

An environmental history of Moreton Bay and its catchment is presented by Neil (1998). Medium to long term changes in the physical and biological environment and in water quality have been noted for parts of Moreton Bay. Personal observations (1972 to present) and anecdotal evidence from 1959 onward suggest a significant accumulation of fine muddy sediments off the Redcliffe Peninsula over this time. This area has

been recognised as a 'hot spot' of high nutrient load, low tidal circulation and declining water quality (Anon., 1997b). Inshore turbidity here was once consistently low, except when strong winds created turbulent conditions, and quickly returned to low levels after winds abated. Around the inshore reefs underwater visibility averaged 5 to 6m throughout the year during light weather. In more recent years sediments have been mobilised by relatively light winds and despite clearer prevailing conditions in the winter months, underwater visibility has rarely exceeded 3m and probably has averaged less than 2m, even in calm conditions. Increased phytoplankton concentrations, spurred primarily by high nitrogen levels, have also lowered light penetration in the water column, causing changes in benthic floral communities. Algal blooms have been reported, particularly during the warmer months after heavy rains. The increasing sediment and nutrient loads borne by this area are more than likely a consequence of rapid urban development and population growth within the surrounding catchment (Skinner et al., 1998) and the resultant increased throughput of nutrient enriched sewage effluent from wastewater plants servicing the northern suburbs of Brisbane, Pine Rivers and Redcliffe. A decline in water quality and habitats broadly across western Moreton Bay and algal blooms in Deception Bay, Bramble Bay and Hayes Inlet have been reported (Abal & Dennison, 1996; Anon., 1997b; Abal et al., 1998; Gabric et al., 1998). Gabric et al. (1998) undertook a two year survey of the water quality of Moreton Bay using in situ studies backed by satellite imagery to describe spatial and temporal variability and the level of eutrophication. Their results confirm a strong east-west gradient in chlorophyll α and water clarity. They found that although tidal intrusion of oceanic water mitigates the impact of high nutrient load in eastern parts of the bay, there is insufficient tidal flushing in the western part of the bay to prevent significant degradation and eutrophication. There are estimates of massive increases in chlorophyll α concentrations over the long term in response to predicted population increase and land use intensification (McEwan et al., 1998). Corresponding with the deterioration in water quality, long term changes in algal, mollusc and fish communities have also been observed, particularly on the littoral and inshore reefs of the Redcliffe Peninsula. Although the once abundant sargassum *Sargassum flavicans* remains common in pockets, filamentous and red algae appear to be increasingly predominant. Many macroalgal species are known to respond either positively or negatively to changes in water quality. Unfortunately the macroalgae of Moreton Bay are poorly known, and to recognise water quality induced changes in communities that are naturally dynamic, more detailed baseline knowledge of natural spatial and temporal variability and relative abundance of species is required (Phillips, 1998). The commercial oyster *Saccostrea commercialis*, once abundant littorally on the red laterite reef of the Redcliffe Peninsula, has almost completely disappeared. Stress caused by high turbidity, sedimentation and/or poor water quality has possibly rendered it more susceptible to infection by the protozoan parasite responsible for QX disease. The decline in oyster populations has been paralleled by an increase in numbers of the hairy mussel *Trichomya hirsutus*. Algal feeding fishes such as Luderick *Girella tricuspidata* and Magpie Morwong *Cheilodactylus vestitus*, once regularly observed in large numbers off Redcliffe, are now very poorly represented in the area. Although a marked fall in observed numbers of some other fish species may arguably be attributable to fishing activity, these species are subject to minimal fishing pressure in the area and remain relatively common in some other parts of Moreton Bay, indicating that the decline in their populations may have resulted from localised environmental and water quality changes.

## HISTORY OF ICHTHYOLOGICAL RESEARCH

Historically, the Queensland Museum has been intimately involved in the documentation of fish fauna in Moreton Bay. It has acted as a repository for numerous specimens taken in the region by both serious collectors and curious fishermen. From his appointment to the QM in 1882 until 1911, Charles de Vis wrote descriptions of 194 new species of fishes (Ingram, 1990), many of which were collected in Moreton Bay. Many of his descriptions were inaccurate, however, and most have been placed into synonymy. James Ogilby also contributed numerous papers, during both his capacity as honorary curator of the Amateur Fishermen's Association of Queensland (1905-1912) and his tenure at the QM between 1912 and 1920. Most of Ogilby's type specimens that had been lodged in the collections of the Amateur Fishermen's Association were

later transferred to the QM. Many of these fishes were taken by AFAQ members and associates in Moreton Bay. Ogilby (1916a) produced a list of fishes from Queensland waters, with some references to Moreton Bay; however this only progressed taxonomically to the family Clupeidae. McCulloch & Whitley (1925) also published a list pertaining to Queensland waters that made mention of 310 species from Moreton Bay. The number of species in this list however, is not reflective of numbers present as it contains many synonymous species, nomen nuda and probable misidentifications. Tom Marshall was employed at the QM primarily as an artificer and modeller from 1912 to 1942, however during this time as well as his tenure at the Department of Harbours and Marine as Assistant Chief Inspector of Fisheries and Government Ichthyologist (1942-1962), he produced a series of ichthyological notes reporting new records of fishes from Queensland. Among these Marshall (1925, 1928, 1941, 1951, 1953, 1957) reported 29 species previously unknown from Moreton Bay. In 1964 he provided a useful guide to the fishes of Queensland, but distributions given were generalised and only scant reference was made of Moreton Bay.

Maclean (1973) documented fishes taken at night from 7 hours 45 minutes of commercial otter trawling near Mud Island in 1966. His list unfortunately aggregates many taxa into generic groupings. Stephenson & Dredge (1976) and Quinn (1980) conducted analyses of estuarine fish assemblages in Serpentine Creek, near the Brisbane R. mouth, recording 42 species. Surveys by Young & Wadley (1979) using a small mesh one metre wide beam trawl yielded an array of 87 species that included numerous small species (especially gobiids) not obtained by other surveys employing larger gear. Blaber & Blaber (1980) studied factors affecting the distribution patterns of 25 species of estuarine and inshore fishes from 4 sites throughout Moreton Bay, each representing different habitat types. They recorded one species, *Hyporhamphus dussumieri* from Kooringal, South Passage, the occurrence of which was not verified by this study. Demersal fishes were sampled, using commercial prawn trawling gear, by Stephenson & Burgess (1980) and Stephenson et al. (1982a, 1982b). They listed 69 species in order of abundance but eliminated from their results additional species occurring in only one sample. Using similar gear, Weng (1988) collected 112 species at 9 sites, but listed only the 21 most common. On Coomera Island (27°51'S), Morton et al. (1987, 1988) periodically sampled saltmarsh pools with 2mm dipnets and the inlet draining a large saltmarsh area with a small mesh fyke net. A combined total of only 24 species were collected, all of which had previously been recorded from the area. Morton (1990) used extensive 18mm block nets and seines to sample tidal mangroves at the mouth of Lota and Tingalpa Creeks. He recorded 42 species, two of which are poorly known in the region. Weng (1990) reported the capture of 86 species from beam trawl surveys of five shallow inshore sites in northwestern Moreton Bay, but only listed the 29 most common species. McKay & Johnson (1990) gave a historical account of the fishes of the Brisbane R., including a checklist of 127 marine and estuarine species. They provided comments on relative abundance both within the river and in Moreton Bay. In comparing juvenile fish communities among mangrove forests, seagrass beds and mudflats in two estuaries of Moreton Bay, Laegdsgaard & Johnson (1995) identified 45 species. Of these, *Spratelloides gracilis* (Schlegel) is almost certainly a misidentification and is excluded here. Intertidal rocky shore fish assemblages from three sites within Moreton Bay were contrasted with two nearby exposed sites outside the bay by Tibbetts et al. (1998). They recorded 13 species from the Moreton Bay sites, two of which (*Parenchelyurus hepburni* and *Bathygobius fuscus*) were previously unknown from the area. The latter species appears from QM surveys to be restricted to waters north from Hervey Bay (25°15'S) and the record is regarded here as a misidentification of *B. kreffti*, a common species which was not recorded in their study. Locally, *Bathygobius kreffti* is abundant in sheltered intertidal rocky and weedy habitats, while *B. cocosensis* is common among wave exposed rock platforms and headlands and *B. laddi* is known from shallow subtidal reefs. Tibbetts & Connolly (1998) reviewed available biological data on the nekton of Moreton Bay and assessed ecological patterns and processes within fish communities and current human impacts. Davie & Hooper (1998), using Queensland Museum database records from Moreton Bay, found a distinct western estuarine-inshore versus eastern marine reefal dichotomy in fish diversity from the distribution patterns.

The checklist presented here adds significantly to the recorded fish fauna of Moreton Bay, expanding the total to 750 species. Selective

comments on relative abundance, range and taxonomic problems are also given.

## METHODS

The fishes listed are those recorded from within Moreton Bay (Fig. 1), the water body to the west of Moreton and Stradbroke Islands, from Comboyuro Point (27°04'S) to the Nerang R. mouth, near Southport (27°59'S). Most records are based on specimens held in the collection of the Queensland Museum. Several, however, are from specimens in the Australian Museum (Sydney) and literature records and 57 are from the author's sight records or personal observations. One record is based on sightings by Barry Hutchins (Curator of Fishes, WAM). Larval fishes were not sampled as part of this study and do not form the basis of any of the records. Where records are not based on registered museum specimens the basis for inclusion is clearly denoted. As it is anticipated that this list is incomplete, collectors of species that constitute additional records are encouraged to lodge voucher specimens in the collection of the Queensland Museum.

Efforts were made to sample or make observations throughout the bay in all habitat types with a wide variety of gear, to enhance coverage. Many specimens came from prior unpublished surveys and miscellaneous donations lodged with the QM. Previous identifications were verified wherever possible. Existing demersal trawl survey material was considered to provide good coverage. QM collections contained fishes taken on otter and beam trawlers by professional collectors and interested trawler operators over many years and species numbers well exceeded those documented by the detailed surveys of Stephenson & Burgess (1980) and Stephenson et al. (1982a, 1982b). Numerous scuba dives were undertaken for underwater visual surveys, collection by spear and rotenone stations. Seine nets of various mesh sizes were employed on tidal flats, beaches and estuarine mudbanks and rotenone was applied in some mangrove creeks and littoral reefs. Dredging with a 1.2m sled fitted with 2mm mesh was carried out to sample small fishes associated with subtidal soft bottom areas in estuarine channels, over seagrass beds and around offshore subtidal sandbanks.

Relative abundance was based on a combination of indicators, including numbers of specimen lots in museum collections and the frequency a species was collected or observed in the field by the author. It is presented according to the following criteria: rare – 1 to 4 records, uncommon – 5 to 9 records, common – 10 to 100 records and abundant – more than 100 records. In general, an observation of a shoal of schooling fish was regarded as a single rather than multiple record of the species. Where species are classed as 'uncommon (or rare) inside Moreton Bay' their abundance was perceived to be relatively greater in adjacent waters immediately outside Moreton Bay. The term 'locally common' is used where species are known to occur commonly in Moreton Bay only at the locations specifically cited. Northern and southern records refer to the end point of distribution on the east coast of Australia, unless stated otherwise. Species that have their coastal southern limit in Moreton Bay, but occur further south in offshore Australian waters at Middleton Reef, Elizabeth Reef, Lord Howe Island or Norfolk Island are so indicated, but retained here in species totals for southern records. Where no distributional limits are given, Moreton Bay falls wholly within the known range of the species. In some cases new extensions of range beyond Moreton Bay are recognised. Worldwide geographic range for each species is briefly summarised. Museum registration numbers are given for species regarded as rare, for voucher specimens of undescribed or indeterminate species and for specimens representing extensions of range.

The checklist generally follows the classification of Paxton et al. (1989). Some comments are given for clarification where current taxonomic problems exist or have been identified. The following abbreviations are used for institutions: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences, San Francisco; USNM, National Museum of Natural History, Washington; NMV, Museum Victoria, Melbourne; NTM, Northern Territory Museum, Darwin; QM, Queensland Museum, Brisbane; WAM, Western Australian Museum, Perth.

## THE FISHES OF MORETON BAY

### DASYATIDIDAE

***Dasyatis kuhlii*** (Müller & Henle, 1841)
Abundant. Tropical Indo-west Pacific.

***Dasyatis fluviorum*** Ogilby, 1908
Common. Subtropical eastern Australia.

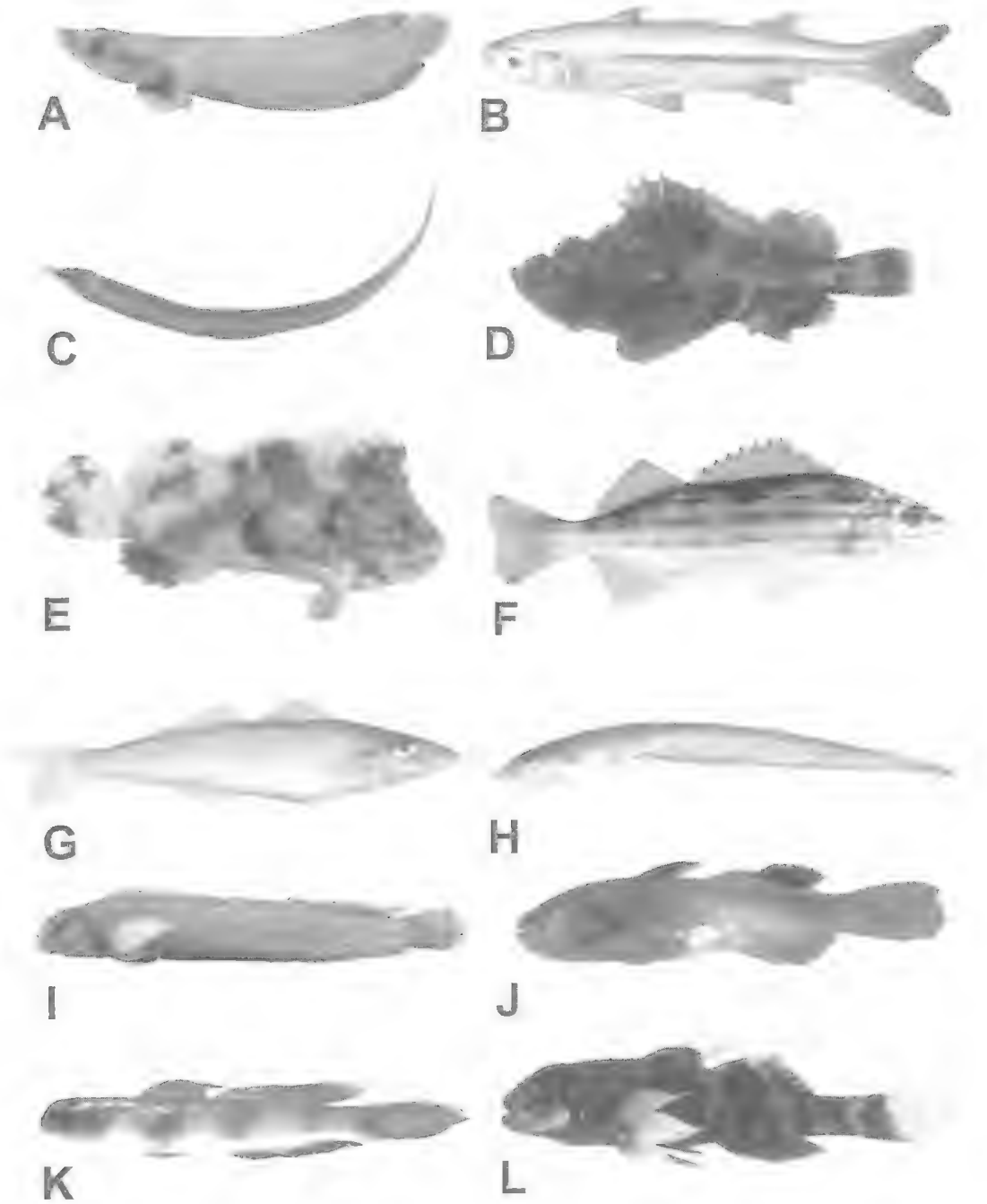



FIG. 2. Some new records of rare fishes from Moreton Bay. A. *Lepadichthys frenatus*, Tangalooma Wrecks. B. *Craterocephalus mugiloides*, Cabbage Tree Ck mouth. C. *Cosmocampus howensis*, Southport seaway. D. *Scorpaenopsis gibbosa*, Myora Reef. E. *Cocotropus* sp., Southport seaway. F. *Helotes sexlineatus*, Manly. G. *Sillago ingenuua*, Pearl Channel. H. *Matsubaraea fusiforme*, Western Banks. I. *Laiphognathus multimaculatus*, Amity Point. J. *Austrolethops wardi*, Dunwich. K. ?*Cryptocentrus* sp., Tangalooma Point. L. *Butis koilomatodon*, Nundah Ck.

***Himantura fai*** Jordan & Seale, 1906
Rare. Reported from Stradbroke I. by Last & Stevens (1994: 401). Southern limit. Tropical Australia to Micronesia.

***Himantura granulata*** (Macleay, 1883)
Rare. Reported by Last & Stevens (1994: 402). Southern limit. Tropical W Pacific and N Australia to Indonesia.

***Himantura*** sp.
Common. Reported as *Himantura* sp. A by Last & Stevens (1994: 398). Southern limit. Northeastern Australia to Darwin.

***Himantura uarnak*** (Forsskål, 1775)
Common. Southern limit. Tropical Indo-west Pacific.

***Pastinachus sephen*** (Forsskål, 1775)
Common. Tropical Indo-west Pacific.

***Taeniura meyeni*** Müller & Henle, 1841
Uncommon. Sight records from Amity Pt and Curtin Artificial Reef. Southern record (excluding Lord Howe and Norfolk I. (Francis, 1993)). Tropical Indo-west Pacific.

GYMNURIDAE

***Gymnura australis*** (Ramsay & Ogilby, 1886)
Common. Tropical Australia.

UROLOPHIDAE

***Trygonoptera testacea*** (Müller & Henle, 1841)
Abundant. Southeastern Australia.

MYLIOBATIDIDAE

***Aetobatus narinari*** (Euphrasen, 1790)
Abundant. Circumtropical.

***Myliobatis australis*** Macleay, 1881
Uncommon. Reported by Last and Stevens (1994) as northern limit. Southern Australia.

***Myliobatis hamlyni*** Ogilby, 1911
Rare. Known in Moreton Bay only from the holotype, whose location was considered by Paxton et al. (1989: 49) to be unknown. As concluded by Whitley (1939), QMI1567 is likely to be the type, as the registration date (Oct. 1913) is close to Ogilby's stated collection date and there are no other examples of the genus in the QM. The specimen, however, is labelled Cape Moreton and is slightly smaller (271mm vs 280mm disc width). Elsewhere, recorded from off Cape Moreton (27°02'S) and Forestier I., WA. Tropical Australia.

RHINOPTERIDAE

***Rhinoptera neglecta*** Ogilby, 1912
Uncommon. Tropical to subtropical eastern Australia.

MOBULIDAE

***Manta birostris*** (Donndorff, 1798)
Uncommon inside Moreton Bay. Sight records only. Circumtropical.

***Mobula eregoodootenkee*** (Cuvier, 1829)
Rare. Reported south to Townsville by Last & Stevens (1994: 461). Two specimens (QMI3008-9) collected from Moreton Bay prior to 1918 but destroyed in 1937 were probably the basis of the record by Ogilby (1916a, 1918b). Extant specimens from 'south Qld' (QMI3419) and Caloundra (26°48'S, QMI4516) were also originally identified by Ogilby. Southern record. Tropical Indo-Australian Archipelago and northern Indian Ocean.

RHINOBATIDAE

***Aptychotrema rostrata*** (Shaw & Nodder, 1794)
Abundant. Warm temperate to subtropical eastern Australia.

***Rhinobatos typus*** Bennett, 1830
Common. Tropical east Indo-west Pacific.

RHYNCHOBATIDAE

***Rhina ancylostoma*** Bloch & Schneider, 1801
Uncommon. Tropical Indo-west Pacific.

***Rhynchobatus djiddensis*** (Forsskål, 1775)
Common. Tropical Indo-west Pacific.

PRISTIDAE

***Pristis zijsron*** Bleeker, 1851
Rare. Highly susceptible to gill netting and trawling, it is now rare in most areas heavily fished. No reports from this area have been received since the 1960s. Tropical Indo-west Pacific.

## TORPEDINIDAE

***Hypnos monopterygium*** (Shaw & Nodder, 1795)
Uncommon inside Moreton Bay. Extends north to Mooloolaba (26°41'S, QMI27498). Temperate to subtropical southeastern and Western Australia.

## ODONTASPIDIDAE

***Carcharias taurus*** Rafinesque, 1810
Uncommon inside Moreton Bay. Temperate to subtropical circumglobal, except eastern Pacific.

## LAMNIDAE

***Carcharodon carcharias*** (Linnaeus, 1758)
Common. Found inside Moreton Bay mainly from May to September. Specimens to 4.5 m total length have been confirmed. Temperate to subtropical circumglobal.

***Isurus oxyrinchus*** Rafinesque, 1810
Uncommon inside Moreton Bay. Circumglobal.

## ALOPIIDAE

***Alopias vulpinus*** (Bonnaterre, 1788)
Rare inside Moreton Bay. Reported by Ogilby (1916a). Occasionally sighted off Pt Lookout, Stradbroke I. Northern record. Circumglobal, mainly in temperate and subtropical seas.

## TRIAKIDAE

***Galeorhinus galeus*** (Linnaeus, 1758)
Rare. Reported from Moreton Bay by Ogilby (1908), Marshall (1964) and Last & Stevens (1994: 208). Impossible to verify as only known specimens (QMI7821-2) have been destroyed. Northern limit. Southern Australia, eastern Pacific, southern and western-north Atlantic.

***Mustelus antarcticus*** Günther, 1870
Uncommon inside Moreton Bay. Temperate to subtropical Australia.

## HEMIGALEIDAE

***Hemigaleus microstoma*** Bleeker, 1852
Common. Tropical east Indo-west Pacific.

## CARCHARHINIDAE

***Carcharhinus brachyurus*** (Günther, 1870)
Uncommon. Two specimens (QMI7976-7) removed from a female taken at Tangalooma and a verified photograph of a 2.8m specimen caught at Bulwer by L. Higgs in 1996. Previously recorded north to Coffs Harbour (Last & Stevens, 1994: 236). Northern record. Unconfirmed reports extend north to Scarness beach, Hervey Bay (25°17'S). Circumglobal, in most temperate and subtropical seas.

***Carcharhinus brevipinna*** (Müller & Henle, 1839)
Abundant. Tropical to warm temperate circumglobal, except eastern Pacific.

***Carcharhinus leucas*** (Valenciennes, 1839)
Common in estuaries and inshore waters. Penetrates upstream to freshwater in the Brisbane R. Circumtropical.

***Carcharhinus limbatus*** (Valenciennes, 1839)
Common. Circumtropical.

***Carcharhinus melanopterus*** (Quoy & Gaimard, 1824)
Doubtful record. Last & Stevens (1994: 251) follow Ogilby (1908b; 1916a) and report Moreton Bay as southern limit. Ogilby's records, however, were from snapper banks, outside Moreton Bay and were almost certainly a misidentification of another *Carcharhinus* species. Ogilby retained no voucher specimens and is reported by Whitley (1934) to have given a length of 10 feet for *C. melanopterus*, much larger than the 140 cm Australian maximum accepted by Last & Stevens (1994). Occurrence south of the Capricorn-Bunker group not verified. Tropical central and Indo-west Pacific.

***Carcharhinus obscurus*** (Lesueur, 1818)
Common. Circumglobal.

***Carcharhinus plumbeus*** (Nardo, 1827)
Common. Circumglobal.

***Carcharhinus sorrah*** (Valenciennes, 1839)
Abundant. Reported south to Gladstone (Last & Stevens, 1994: 255). Personal observations (1978-92) indicated that this was easily the most common carcharhinid species in Moreton Bay. Specimens (including late term pregnant females) were commonly taken from October to

April in Moreton Bay. Southern record QMI-14073. Tropical Indo-west Pacific.

***Galeocerdo cuvier*** (Pèron & Lesueur, 1822)
Common. Circumtropical.

***Loxodon macrorhinus*** Müller & Henle, 1839
Rare. Southern record QMI5166. Tropical Indo-west Pacific.

***Negaprion acutidens*** (Rüppell, 1837)
Common. Southern record QMI8254, from Southport. Tropical central and Indo-west Pacific.

***Rhizoprionodon acutus*** (Rüppell, 1837)
Common. Southern record QMI14071-2. Tropical Indo-west Pacific and eastern Atlantic.

***Rhizoprionodon taylori*** (Ogilby, 1915)
Common. Southern record QMI14909. Tropical Australia.

SPHYRNIDAE

***Sphyrna lewini*** (Griffith & Smith, 1834)
Abundant. Record of *S. zygaena* (Linnaeus, 1758) from Moreton Bay by McCulloch & Whitley (1926) was probably a misidentification of this species. Northern limit of *S. zygaena* reported by Last and Stevens (1994: 276) is near Coffs Harbour, NSW (33°00'S). Circumglobal in tropical to warm temperate seas.

***Sphyrna mokarran*** (Rüppell, 1837)
Rare inside Moreton Bay. Only record a verified photograph of a 3.6m specimen taken at Bulwer by S. Goleby on 5/1/1995. Circumtropical.

ORECTOLOBIDAE

***Brachaelurus colcloughi*** Ogilby, 1908
Common. Patchy distribution between Coolangatta (28°10'S) and off Gladstone (23°26'S) and off Cape York Peninsula (Last & Stevens, 1994: 123). Relatively rare outside Moreton Bay region. Subtropical Qld.

***Brachaelurus waddi*** Bloch & Schneider, 1801
Uncommon. Reported north to Moreton Bay by Last & Stevens (1994: 124). QM records extend to Mudjimba I. (26°37'S, QMI29110). Warm temperate to subtropical eastern Australia.

***Chiloscyllium punctatum*** Müller & Henle, 1838
Abundant. Tropical east Indo-west Pacific.

***Orectolobus maculatus*** (Bonnaterre, 1788)
Common. Northern record QMI226. Temperate to subtropical Australia.

***Orectolobus ornatus*** (De Vis, 1883)
Abundant. Southern and eastern Australia, to New Guinea.

***Stegostoma fasciatum*** (Hermann, 1783)
Common. Tropical to subtropical Indo-west Pacific.

HETERODONTIDAE

***Heterodontus galeatus*** (Günther, 1870)
Rare. Two specimens QMI4017 and QMI5104. Occurs north to near Cape Moreton (26°56'S, QMI13003). Warm temperate eastern Australia.

***Heterodontus portusjacksoni*** (Meyer, 1793)
Rare. Recorded from Moreton Bay by Saville-Kent (1897: 193) and included by Marshall (1964), but not verified by specimens and possibly a misidentification of *H. galeatus*. Northern limit. Southern Australia.

ELOPIDAE

***Elops hawaiensis*** Regan, 1909
Common. Tropical central and east Indo-west Pacific.

***Megalops cyprinoides*** (Broussonet, 1782)
Common. Tropical Indo-west Pacific.

ALBULIDAE

***Albula neoguinaica*** Valenciennes, 1847
Uncommon inside Moreton Bay. *Albula argentea* (Forster, 1801) may be a senior synonym (Randall et al., 1997: 32). Tropical to subtropical Indo-west Pacific.

NETTASTOMATIDAE

***Saurenchelys finitimus*** (Whitley, 1935)
Rare. Southern record QMI30249. Northeastern Australia.

## OPHICHTHIDAE

***Malvoliophis pinguis*** (Günther, 1872)
Common. Eastern Australia to Melanesia.

***Muraenichthys cf laticaudatus*** (Ogilby, 1897)
Common. Six lots in QM, all collected from muddy or fine silty substrate. These specimens compare closely with *M. godeffroyi* Regan, however this is regarded as a probable junior synonym of *M. laticaudatus* by McCosker (1970). *M. laticaudatus* is reported south to Capricorn Group by Paxton et al. (1989: 118), Middleton and Elizabeth Reefs (noteably as cryptic reef dweller) by Gill & Reader (1992: 195) and Lord Howe I. by Francis (1993). Differences in morphometrics and habitat preference suggest the Moreton Bay specimens may represent the southern record of a distinct species. Tropical Indo-west Pacific?

***Muraenichthys macropterus*** Bleeker, 1857
Rare. Recorded south to Capricorn Group by Paxton et al. (1989: 118). Southern record QMI30226 from Redcliffe. Tropical Indo-west Pacific.

***Ophichthus episcopus*** Castelnau, 1878
Rare. Only known from the holotype which is reported to have been lost (Paxton et al., 1989). Moreton Bay.

***Ophichthus*** sp.
Rare. Only record QMI14562. Possibly conspecific with *O. episcopus*. Moreton Bay.

***Ophisurus serpens*** (Linnaeus, 1758)
Rare. Paxton et al. (1989: 120) recorded Grafton (29°41'S) as northern limit. Extends to at least Noosa R. (26°24'S, QMI9087). Temperate to subtropical circumglobal.

## ANGUILLIDAE

***Anguilla australis*** Richardson, 1841
Common. Usually collected in freshwater. Southeastern Australia.

***Anguilla reinhardtii*** Steindachner, 1867
Abundant. Adults as well as migrating elvers of *Anguilla* spp. are found commonly in the lower estuary as well as in freshwater. Eastern Australia and New Caledonia.

## MURAENIDAE

***Echidna polyzona*** (Richardson, 1845)
Rare. Only records QMI8964 and QMI31149. Central and Indo-west Pacific.

***Gymnothorax boschii*** (Bleeker, 1853)
Rare. Reported south to Capricorn Group by Paxton et al. (1989: 128). Two specimens, QMI29260 from Tangalooma Wrecks and QMI30225 from Redcliffe. Southern record. Tropical West Pacific and Indo-Malay Archipelago.

***Gymnothorax cribroris*** Whitley, 1932
Common. Subtropical eastern Australia.

***Gymnothorax eurostus*** (Abbott, 1860)
Locally common at Amity Pt. Tropical central and Indo-west Pacific.

***Gymnothorax favagineus*** Bloch & Schneider, 1801
Common. Tropical Indo-west Pacific.

***Gymnothorax fimbriatus*** (Bennett, 1832)
Rare. Reported south to Capricorn Group by Paxton et al. (1989: 129). Sight record from Tangalooma Wrecks only. Southern record. Tropical Indo-west Pacific.

***Gymnothorax meleagris*** (Shaw & Nodder, 1795)
Doubtful record. No specimens in QM. Reported by Paxton et al. (1989: 130) as southern limit. Possibly a misidentification of *G. eurostus*. Tropical Indo-Pacific.

***Gymnothorax prasinus*** (Richardson, 1848)
Rare. Reported north to Byron Bay by Paxton et al. (1989: 131) and southern Qld by Hutchins & Swainston (1986: 30). Northern record QMI31175 from Southport seaway. Southwest Pacific, southeastern and southwestern Australia.

***Gymnothorax pseudothyrsoideus*** (Bleeker, 1852)
Abundant. Tropical west Pacific.

***Gymnothorax undulatus*** (Lacepède, 1803)
Rare. Reported south to Capricorn Group by Paxton et al. (1989: 132). Southern record QMI30222 from Redcliffe. Tropical Indo-Pacific.

***Gymnothorax*** sp.
Rare. Unidentified species similiar to *G. cribroris* but lacking characteristic black spots on head. Known only from three specimens taken in

southern Qld. Figured in Grant (1987: pl.106a). Currently under study by E. Bohlke (ANSP) and J. McCosker (CAS). Southern record QMI5141. Southeast Qld.

***Thyrsoidea macrura*** (Bleeker, 1854)
Uncommon. *Strophidon sathete* (Hamilton, 1822) may be a senior synonym (Randall et al., 1997: 42). Six QM specimens from Moreton Bay. Southern record QMI3360 from Coomera R. Tropical Indo-west Pacific?

CONGRIDAE

***Ariosoma anago*** (Temminck & Schlegel, 1847)
Rare inside Moreton Bay. Only records QMI-13632 and QMI30693. Tropical east Indo-west Pacific.

***Conger cinereus*** Rüppell, 1830
Rare. Reported south to One Tree I. by Paxton et al. (1989: 141). Southern record QMI30296 from Dunwich, excluding Elizabeth Reef (Gill & Reader, 1992: 194) and Lord Howe I. (Francis, 1993). Tropical central and Indo-west Pacific.

***Conger wilsoni*** (Bloch and Schneider, 1801)
Uncommon. Northern record QMI29718 from Deception Bay. Temperate to subtropical west Pacific and southern Indian Ocean.

MURAENESOCIDAE

***Muraenesox bagio*** (Hamilton, 1822)
Common. Tropical Indo-west Pacific.

CLUPEIDAE

***Herklotsichthys castelnaui*** (Ogilby, 1897)
Abundant. Eastern Australia.

***Herklotsichthys koningsbergeri*** (Weber & de Beaufort, 1912)
Common. Tropical to subtropical Australia.

***Hyperlophus translucidus*** McCulloch, 1917
Abundant. Southeastern Australia.

***Hyperlophus vittatus*** (Castelnau, 1875)
Uncommon inside Moreton Bay. Reported by Paxton et al. (1989: 155) based on AMS specimens from Southport (AMIA6916) and Pt Lookout (AMI12595). Northern limit. Temperate to subtropical Australia.

***Nematalosa erebi*** (Günther, 1868)
Abundant. Freshwater/estuarine species commonly found near Brisbane R mouth. Rivers of northern to south-central Australia and southwestern Papua New Guinea.

***Sardinella gibbosa*** (Bleeker, 1849)
Common. Indo-west Pacific.

***Sardinops sagax neopilchardus*** (Steindachner, 1879)
Common. Temperate to subtropical southwest Pacific and southwestern Australia.

***Spratelloides delicatulus*** (Bennett, 1832)
Common. Reported south to One Tree I. by Paxton et al. (1989: 157). Southern record QMI31311 from Amity Pt, excluding Norfolk I. (Francis, 1993). Tropical Indo-west Pacific.

***Spratelloides robustus*** Ogilby, 1897
Common. Subtropical to temperate southern Australia.

ENGRAULIDIDAE

***Engraulis australis*** (White, 1790)
Common. Subtropical to temperate southwest Pacific and southwestern Australia.

***Stolephorus carpentariae*** (De Vis, 1883)
Common. Southern record QMI26090 from Aldershots (27°51'S). Tropical to subtropical Australia.

***Thryssa aestuaria*** (Ogilby, 1910)
Common. Often confused with *T. hamiltonii*. Tropical to subtropical Australia and New Guinea.

***Thryssa hamiltonii*** (Gray, 1835)
Rare. Rank of twentieth in abundance of trawled fishes in Moreton Bay ascribed by Stephenson and Burgess (1980) may be a misidentification and probably should be attributed to *T. aestuaria*. Only one record, QMI248, confirmed from Brisbane R. Southern record. Tropical Indo-west Pacific.

CHIROCENTRIDAE

***Chirocentrus dorab*** (Forsskål, 1775)
Rare. Two records only, QMI4945 and QMI8051. Southern limit. Tropical central and Indo-west Pacific.

GALAXIIDAE

***Galaxias maculatus*** (Jenyns, 1842)
Rare. Occasional specimens taken at creek mouths on Russell and Stradbroke Is. Northern record QMI28115 from Myora Ck. Adults in freshwater, larvae and juveniles pelagic marine. Temperate circumglobal, except South Africa.

GONORYNCHIDAE

***Gonorynchus greyi*** (Richardson, 1845)
Uncommon inside Moreton Bay. Temperate to subtropical Australia.

CHANIDAE

***Chanos chanos*** (Forsskål, 1775)
Uncommon. Tropical to warm temperate central and Indo-west Pacific.

ARIIDAE

***Arius graeffei*** Kner & Steindachner, 1866
Abundant. Tropical to subtropical Australia and New Guinea.

***Arius macrocephalus*** Bleeker, 1846
Uncommon. Two specimens QMI11502 and QMI31170 from Brisbane R. Southern limit. Northern Australia and Indo-Malay Archipelago.

***Arius proximus*** Ogilby, 1898
Common. Tropical to subtropical Australia and west Pacific.

PLOTOSIDAE

***Cnidoglanis macrocephalus*** (Valenciennes, 1840)
Uncommon. Reported from Brisbane R. by Thomson (1978). Specimen, QMI30306 from Southport seaway. Northern record. Southeastern and southwestern Australia.

***Euristhmus lepturus*** (Günther, 1864)
Common. Subtropical Australia to New Guinea.

***Euristhmus nudiceps*** (Günther, 1880)
Rare. Reported from Brisbane by Paxton et al. (1989: 224) as southern limit. Record not verified and possibly a misidentification of *E. lepturus*. Tropical Australia to New Guinea.

***Paraplotosus albilabrus*** (Valenciennes, 1840)
Rare. Reported south to One Tree I. (23°30'S) by Paxton et al. (1989: 225). Southern record QMI30220 from Redcliffe. Tropical Australia and west Pacific.

***Plotosus lineatus*** (Thunberg, 1791)
Abundant. Tropical Indo-west Pacific.

SYNODONTIDAE

***Synodus dermatogenys*** Fowler, 1912
Locally common at Curtin Artificial Reef. Voucher QMI31005. Tropical central and Indo-west Pacific.

***Trachinocephalus myops*** (Forster, 1801)
Common. Atlantic and central to Indo-west Pacific.

HARPADONTIDAE

***Harpadon translucens*** Saville-Kent, 1889
Uncommon. Occasional specimens taken near Brisbane and Caboolture R. mouths. Southern record QMI28606. Tropical Australia to New Guinea.

***Saurida gracilis*** Quoy & Gaimard, 1824
Uncommon inside Moreton Bay. Reported south to One Tree I. by Paxton et al. (1989: 243). Southern record QMI31168 from Southport seaway, excluding Lord Howe and Norfolk I. (Francis, 1993; Francis & Randall, 1993). Tropical central and Indo-west Pacific.

***Saurida tumbil*** (Bloch, 1795)
Common. Tropical Indo-west Pacific.

***Saurida undosquamis*** (Richardson, 1848)
Common. Tropical Indo-west Pacific.

BATRACHOIDIDAE

***Batrachomoeus dubius*** (White, 1790)
Common. Central eastern Australia.

***Halophryne queenslandiae*** (De Vis, 1882)
Uncommon. Five specimens in QM. Paxton et al. (1989: 272) recorded southern limit as Brisbane R. mouth. Kuiter (1993) reported distribution as extending into NSW (South Solitary Is., Kuiter pers. comm., 1996). Ogilby (1908c) recorded *Coryziehthys (= Halophryne) diemensis* (Lesueur, 1824) as 'by no means scarce in

Moreton Bay'. *H. diemensis* is known only as far south as the Capricorn Group (23°30'S), according to Paxton et al. (1989: 272) and QM records. In accordance with Hutchins (1976), Ogilby's record of *H. diemensis* from Moreton Bay is considered a misidentification of *H. queenslandiae*. Subtropical to tropical eastern Australia.

ANTENNARIIDAE

***Antennarius coccineus*** (Lesson, 1830)

Rare. Only records QMI363 (holotype of *A. stigmaticus* Ogilby, 1912), QMI31133 from Southport seaway and QMI31350 from Amity Pt. Tropical central and Indo-west Pacific.

***Antennarius pictus*** (Shaw & Nodder, 1794)

Rare. Only records QMI4462 from Wynnum and QMI29810 from Curtin Artificial Reef. Tropical Indo-west Pacific.

***Antennarius striatus*** (Shaw, 1794)

Common. Tropical Indo-west Pacific.

***Histrio histrio*** (Linnaeus, 1758)

Common. Circumtropical.

GOBIESOCIDAE

***Lepadichthys frenatus*** Waite, 1904

Rare. Only record QMI29162 from Tangalooma Wrecks (Fig. 2A). Occurs south to South Solitary Is., NSW (30°11'S, AMSI22881-001) and Lord Howe and Norfolk I. (Francis, 1993). Tropical west Pacific.

EXOCOETIDAE

***Cheilopogon pinnatibarbatus melanocercus*** (Ogilby, 1885)

Common. Southwestern Pacific.

***Hirundichthys oxycephalus*** (Bleeker, 1852)

Uncommon inside Moreton Bay. Tropical Indo-west Pacific.

***Parexocoetus brachypterus*** (Richardson, 1846)

Rare. Southern record QMI5379. Tropical Atlantic and central to Indo-west Pacific.

HEMIRHAMPHIDAE

***Arrhamphus sclerolepis krefftii*** (Steindachner, 1867)

Abundant. Subtropical eastern Australia.

***Hemiramphus robustus*** Günther, 1866

Common. Tropical to temperate Australia, excluding Great Australian Bight.

***Hyporhamphus australis*** (Steindachner, 1866)

Uncommon. Northern record QMI11501. Southeastern Australia.

***Hyporhamphus quoyi*** (Valenciennes, 1847)

Common. Tropical Indo-west Pacific.

***Hyporhamphus regularis ardelio*** (Whitley, 1931)

Abundant. Temperate and subtropical eastern Australia.

BELONIDAE

***Ablennes hians*** (Valenciennes, 1846)

Uncommon inside Moreton Bay. Tropical to subtropical circumglobal.

***Strongylura leiura*** (Bleeker, 1851)

Uncommon. Three specimens in QM. Reported by Morton (1990) from Tingalpa Ck mouth. Temperate to tropical Indo-west Pacific.

***Tylosurus acus*** (Lacepède, 1803)

Rare inside Moreton Bay. The single record of *T. appendiculatus* (Klunzinger, 1871) reported by Marshall (1964) is probably referable to this species. Circumtropical.

***Tylosurus crocodilus*** (Péron & Lesueur, 1821)

Rare. Reported as southern limit by Paxton et al. (1989: 343). No specimens in QM. Circumtropical.

***Tylosurus gavialoides*** (Castelnau, 1873)

Abundant. Tropical to subtropical Australia.

PSEUDOMUGILIDAE

***Pseudomugil signifer*** Kner, 1867

Common near mouths of most estuarine streams flowing into Moreton Bay as well as the freshwater reaches. Tropical to warm temperate eastern Australia.

## ATHERINIDAE

***Craterocephalus honoriae*** (Ogilby, 1912)
Rare. Occurs in estuaries. Only record AMSIB-1340. Reported north to Moreton Bay by Crowley and Ivantsoff (1988). QM records extend to Noosa (26°26'S, QMI23447). Temperate to subtropical eastern Australia.

***Craterocephalus mugiloides*** (McCulloch, 1912)
Rare. Common north from Hervey Bay (25°18'S).

Two records only, from Toorbul (27°04'S) and Cabbage Tree Ck mouth (Fig. 2B). Southern record QMI30987. Tropical Australia.

***Atherinomorus ogilbyi*** (Whitley, 1930)
Abundant. Temperate to subtropical eastern and Western Australia.

***Hypoatherina tropicalis*** (Whitley, 1948)
Locally common off the western beaches of Moreton I. Southwest Pacific.

## MONOCENTRIDIDAE

***Cleidopus gloriamaris*** De Vis, 1882
Common. Temperate to subtropical Australia.

## TRACHICHTHYIDAE

***Optivus*** sp.
Rare inside Moreton Bay. Gomon et al. (1994) stated that this species is distinct from *O. elongatus* (Günther, 1859) from Lord Howe I. and New Zealand. Reported by Ogilby (1912) based on one specimen, QMI782 trawled in 1889. Frequently trawled in deep water off Cape Moreton. Occurs north to off Noosa (26°23'S, QMI30344). Southeastern Australia.

***Trachichthys australis*** Shaw, 1799
Rare. One specimen collected in 1912 by Ogilby at Pimpama I. Northern record QMI663. Temperate Australia.

## BERYCIDAE

***Centroberyx affinis*** (Günther, 1859)
Rare inside Moreton Bay. One specimen, QMI-4921 collected in 1932. Common in deeper water east of Cape Moreton. Reported north to Moreton Bay by Paxton et al. (1989: 375). Extends to at least Fraser I. (25°27'S, QMI19340). Temperate Australia and southwest Pacific.

## HOLOCENTRIDAE

***Myripristis berndti*** Jordan & Evermann, 1903

Locally common at Comboyuro Pt but not recorded elsewhere inside Moreton Bay. Specimens from southern Qld and New South Wales are more melanistic and differ slightly in a number of characters from other populations of this species (Randall & Greenfield, 1996). Very closely related to and often misidentified as *M. murdjan* (Forsskål, 1775). Voucher QMI31007. Tropical central and Indo-west Pacific.

***Sargocentron diadema*** (Lacepède, 1802)

Uncommon inside Moreton Bay. Tropical Indo-west Pacific.

***Sargocentron rubrum*** (Forsskål, 1775)

Uncommon inside Moreton Bay. Specimens from Comboyuro Pt and Myora. Tropical central and Indo-west Pacific.

## ZEIDAE

***Zeus faber*** Linnaeus, 1758

Rare. Reported north to Moreton Bay by Paxton et al. (1989: 390). Extends to at least off Swain Reefs (22°02'S, QMI21563). Temperate east Atlantic and Indo-west Pacific.

## TRACHIPTERIDAE

***Trachipterus arawatae*** Clarke, 1881

Rare. Two specimens, QMI3714 and QMI10153 washed up on beach at Southport. The former is reported by Marshall (1964) as *T. jacksonensis* (Ramsay). A deepwater pelagic species. Temperate southwest Pacific.

## REGALECIDAE

***Regalecus glesne*** Ascanius, 1772

Rare. Two specimens, QMI9626 and QMI9637 found on beach at Southport. A live, but incapacitated specimen was recorded (as *R. pacificus*, Haast) from Comboyuro, Moreton I. by Marshall (1964). Oceanic species occasionally found inshore. Northern record. Temperate circumglobal.

AULOSTOMIDAE

***Aulostomus chinensis*** (Linnaeus, 1766)
Uncommon inside Moreton Bay. One specimen and a sight record from Comboyuro Pt. Tropical Indo-Pacific.

*FISTULARIIDAE*

***Fistularia commersonii*** Rüppell, 1838
Common. Tropical Indo-Pacific.

***Fistularia petimba*** Lacepède, 1803
Common. Tropical and temperate Atlantic and central to Indo-west Pacific.

CENTRISCIDAE

***Centriscus scutatus*** Linnaeus, 1758
Common. *C. cristatus* De Vis, 1885 is a probable synonym as distinguishing characters appear to merge with growth (Paxton et al., 1989: 410). Southern limit. Tropical Indo-west Pacific.

SYNGNATHIDAE

***Campichthys tryoni*** (Ogilby, 1890)
Common. Subtropical to temperate southeastern Australia.

***Choeroichthys brachysoma*** (Bleeker, 1855)
Rare. Reported south to Masthead I. by Paxton et al. (1989: 414). Southern record QMI19771 from Myora. Tropical central and Indo-west Pacific.

***Choeroichthys suillus*** (Whitley, 1951)
Rare. Reported south to Bowen by Paxton et al. (1989: 414). Southern record QMI30285 from Dunwich. Tropical to subtropical Australia.

***Cosmocampus howensis*** (Whitley, 1948)
Rare. In Australian waters, reported only from Jervis Bay and Lord Howe I. (Paxton et al., 1989: 416) and Middleton Reef (Gill & Reader, 1992). Northern record two specimens from Southport seaway, QMI31167 (Fig. 2C). Temperate to subtropical eastern Australia and southwest Pacific.

***Filicampus tigris*** (Castelnau, 1879)
Common. Subtropical to temperate Australia.

***Hippichthys cyanospilus*** (Bleeker, 1854)
Common. Southern record QMI13398 from Welsby (27°24'S). Tropical Indo-west Pacific.

***Hippichthys penicillus*** (Cantor, 1849)
Common. Tropical Indo-west Pacific.

***Hippocampus planifrons*** Peters, 1877
Common historically, but from anecdotal evidence and recent surveys, populations appear to have declined significantly since the 1960s. Paxton et al. (1989: 422) reported *H. zebra* Whitley, 1964 from Moreton Bay from a single paratype (AMIB2819). This paratype is the 'zebra' colour form of *H. planifrons* which is known from Moreton Bay. Southern record QMI26197 from Peel I. Tropical Australia.

***Hippocampus whitei*** Bleeker, 1855
Common. Temperate to subtropical Australia.

***Microphis manadensis*** (Bleeker, 1856)
Doubtful record. The holotype of *Doryichthys stictorhynchus* Ogilby, 1912 (QMI1552) is the only known specimen from Moreton Bay and Australia. Elsewhere distributed from Solomon Islands, northern Papua New Guinea, Indonesia to Taiwan (Dawson, 1985). Collection data possibly confused by Ogilby. Tropical west Pacific.

***Solegnathus dunckeri*** Whitley, 1927
Uncommon inside Moreton Bay. Regularly washed up on nearby ocean beaches. Central eastern Australia.

***Stigmatopora nigra*** Kaup, 1856
Common. Tangalooma Pt reported as northern limit by Paxton et al. (1989: 430). Extends to Mooloolaba (26°40'S, QMI7751). Southwest Pacific and southern Australia.

***Syngnathoides biaculeatus*** (Bloch, 1785)
Common. Tropical central and Indo-west Pacific.

***Urocampus carinirostris*** Castelnau, 1872
Abundant, in seagrass beds. Subtropical to temperate Australia.

***Vanacampus margaritifer*** (Peters, 1869)
Rare. Reported north to Southport (Dawson, 1985). Northern record QMI30885 from Dunwich. Temperate eastern and western Australia.

PEGASIDAE

***Pegasus volitans*** Linnaeus, 1758
Common. *Parapegasus natans* (Linnaeus, 1766) is a junior synonym. Tropical Indo-west Pacific.

SCORPAENIDAE

***Apistops caloundra*** (De Vis, 1886)
Uncommon. Reported south to Caloundra by Paxton et al. (1989: 439). Southern record QMI10825 from Southport. Tropical Australia.

***Centropogon australis*** (White, 1790)
Abundant. Subtropical to temperate eastern and western Australia.

***Centropogon marmoratus*** Günther, 1862
Abundant. Contrary to Paxton et al. (1989: 439), considered distinct from *C. australis* due to differences in squamation, colour and dorsal fin height. Subtropical to temperate eastern Australia.

***Cottapistus praepositus*** (Ogilby, 1903)
Common. Southern record QMI29765 from Amity Pt. Tropical east Indo-west Pacific.

***Dendrochirus zebra*** (Cuvier, 1829)
Common. Tropical Indo-west Pacific.

***Erosa erosa*** (Langsdorf, 1829)
Rare inside Moreton Bay. Reported south to Moreton Bay by Paxton et al. (1989: 441). Southern limit off Coffs Harbour, NSW (30°18'S, K. Graham pers. comm., 1996). Tropical east Indo-west Pacific.

***Hypodytes carinatus*** (Bloch & Schneider, 1801)
Uncommon. Reported south to off Clarence R. (29°26'S) and Newcastle (33°00'S), NSW by Graham & Wood (1997). Tropical east Indo-west Pacific.

***Inimicus caledonicus*** (Sauvage, 1878)
Locally common along the south-western banks of Moreton I. Reported south to Capricorn Group (Paxton et al., 1989: 442). Southern limit Brunswick Heads, NSW (28°32'S, K. Graham pers. comm., 1996). Tropical east Indo-west Pacific.

***Minous versicolor*** Ogilby, 1910
Common, in trawls. Reported south to Albatross Bay by Paxton et al. (1989: 444). Southern limit extended south to off Clarence R., NSW (29°26'S) by Graham & Wood (1997). Tropical Australia.

***Notesthes robusta*** (Günther, 1860)
Common. Usually found in estuaries or freshwater. Tropical to temperate eastern Australia.

***Parascorpaena picta*** Kuhl & van Hasselt, 1829
Rare. *Sebastapistes bynoensis* (Richardson, 1845) is a junior synonym (Paxton et al., 1989: 449). Reported south to Bargara by Paxton et al. (1989: 449). Southern record QMI29254 from Tangalooma Wrecks. Tropical Indo-west Pacific.

***Pterois volitans*** (Linnaeus, 1758)
Common. Tropical central and Indo-west Pacific.

***Scorpaena cardinalis*** Richardson, 1842
Common. Reported north to Moreton Bay by Paxton et al. (1989: 447). Occurs north to at least Fraser I. (25°13'S, personal observations, 1995). Southwest Pacific.

***Scorpaenodes guamensis*** Quoy & Gaimard, 1824
Common. Reported south to Capricorn Group (23°30'S) by Paxton et al. (1989: 449). Southern record QMI31144 from Southport seaway, excluding Middleton Reef (Gill & Reader, 1992) and Norfolk I. (Francis, 1993). Tropical central and Indo-west Pacific.

***Scorpaenodes scaber*** (Ramsay & Ogilby, 1886)
Common. Reported north to Woody Head, NSW (29°22'S) by Paxton et al. (1989: 450). Recorded north to Flinders Reef (26°58'S), QMI25731. Temperate to subtropical eastern Australia.

***Scorpaenopsis gibbosa*** (Bloch & Schneider, 1801)
Rare. Two specimen lots in QM (Fig. 2D). Reported south to Capricorn Group by Paxton et al. (1989: 451). Report from Middleton Reef (29°26'S) by Gill & Reader (1992: 200) is based on a misidentification of QMI22976, *S. diabolus* Cuvier. Southern record QMI31136 from Southport seaway. Tropical Indo-west Pacific.

***Scorpaenopsis macrochir*** Ogilby, 1910
Uncommon. Southern record QMI30376 from Myora. Tropical eastern Australia.

***Scorpaenopsis venosa*** (Cuvier, 1829)
Uncommon. *S. palmeri* Ogilby, 1910 is a junior synonym (Eschmeyer & Rama Rao, in litt.,

1983). Southern record QMI7945 from Amity Pt. Tropical east Indo-west Pacific.

***Synanceia horrida*** (Linnaeus, 1766)
Common. Reported south to Bargara by Paxton et al. (1989: 452). Reports extend to Tweed River, NSW (28°11'S). Tropical east Indo-west Pacific.

***Taenianotus triacanthus*** Lacepède, 1802
Uncommon. Juveniles reported south to Sydney by Kuiter (1993). Tropical central and Indo-west Pacific.

TRIGLIDAE

***Chelidonichthys kumu*** (Lesson, 1826)
Uncommon inside Moreton Bay. Reported north to Brisbane by Paxton et al. (1989: 454). Extends north to off Bunker Group (23°59'S), QMI19293. Temperate to subtropical Indo-west Pacific.

***Lepidotrigla argus*** Ogilby, 1910
Common. Usually trawled along the east channel, inside Moreton Bay but abundant in deeper grounds off Cape Moreton. The records of *L. calodactyla* Ogilby, 1910 by Stephenson & Burgess (1980) and *Paratrigla (= Lepidotrigla) papilio* (Cuvier, 1829) by Weng (1988) are probably misidentifications of this species. Subtropical eastern to tropical western Australia.

APLOACTINIDAE

***Adventor elongatus*** (Whitley, 1952)
Rare. Southern record QMI19066 from Brisbane R. mouth. Tropical Australia.

***Bathyaploactis curtisensis*** Whitley, 1933
Common. Reported south to Port Curtis by Paxton et al. (1989: 460). Some QM specimens from Moreton Bay were identified as *Karumba (=Bathyaploactis) ornatissimus* (Whitley, 1933) by Poss in 1978. These specimens are indiscernible from *B. curtisensis* and are treated here as conspecific. Southern record QMI30913 from Coomera R. Tropical Australia.

***Cocotropus*** sp.
Rare. Probably undescribed species, characterised by velvety skin covered in scales each bearing a spine; dorsal fin elements XII/8; anal fin elements II/6 and pectoral fin rays 11. Dorsal fin moderately elevated at front, middle and rear but not separated or strongly notched and membrane not incised as in *Neoaploactis tridorsalis* Eschmeyer & Allen, 1978. One specimen, QMI31134, from Southport seaway (Fig. 2E). Also known from QMI22142 from Cook Is., NSW (28°12'S). Southeast Qld.

***Paraploactis trachyderma*** Bleeker, 1865
Common. Southern limit Southport (Paxton et al., 1989: 461). Tropical to subtropical eastern Australia and central South Australia.

***Peristrominous dolosus*** Whitley, 1952
Rare. Southern record QMI10720 from Brisbane R. Tropical Australia.

PATAECIDAE

***Pataecus fronto*** Richardson, 1844
Uncommon. Occurs north to at least Alexandra Headland (26°40'S, QMI4519). Temperate to subtropical eastern and southwestern Australia.

PLATYCEPHALIDAE

***Ambiserrula jugosus*** (McCulloch, 1914)
Common. Subtropical eastern Australia.

***Cymbacephalus nematophthalmus*** (Günther, 1860)
Common. Tropical east Indo-west Pacific.

***Cymbacephalus staigeri*** (Castelnau, 1875)
Doubtful record. Reported south to Brisbane by Paxton et al. (1989: 471). Possibly a misidentification of *C. nematophthalmus*. QM records reach south only to Great Keppell I. (23°10'S). Tropical Australia and New Guinea.

***Inegocia harrisii*** (McCulloch, 1914)
Doubtful record. Reports by Stephenson & Burgess (1980), Stephenson et al. (1982a) and others are almost certainly misidentifications of *I. japonica* (Tilesius). *Inegocia harrisii* was described by McCulloch from two syntypes, AMSE2844 from near Pine Peak, Qld and AMSI12765 from Moreton Bay, however the latter is a specimen of *I. japonica* (Johnson, 1999). Distribution as recognised by Paxton et al. (1989: 466), Pine Peak, Qld (21°31'S) north to Napier Broome Bay, WA (126°36'E). Tropical Australia.

***Inegocia japonica*** (Tilesius, 1812)
Common, in trawls. Often misidentified as *I. harrisii* (see note above). Southern limit. Tropical east Indo-west Pacific.

***Levanaora bosschei*** (Bleeker, 1860)
Rare. Reported south to One Tree I. by Paxton et al. (1989: 471). Southern record QMI11525. Tropical Indo-west Pacific.

***Platycephalus arenarius*** Ramsay & Ogilby, 1886
Abundant. Tropical Indo-Australian Archipelago.

***Platycephalus caeruleopunctatus*** McCulloch, 1922
Uncommon inside Moreton Bay. Commonly taken off Southport. Temperate eastern Australia.

***Platycephalus endrachtensis*** Quoy & Gaimard, 1824
Common. Often confused with *P. indicus*. Tropical Australia and New Guinea.

***Platycephalus fuscus*** Cuvier, 1829
Abundant. Temperate to tropical eastern Australia.

***Platycephalus indicus*** (Linnaeus, 1758)
Common. Tropical Indo-west Pacific.

***Platycephalus longispinis*** Macleay, 1884
Common. Temperate to subtropical eastern and southwestern Australia.

***Sorsogona tuberculata*** (Cuvier, 1829)
Rare. Two specimens, QMI30684 from near Shark Spit, Moreton I. Reported south to Platypus Bay (24°56'S) by Paxton et al. (1989: 470). Southern record. Tropical Indo-west Pacific.

***Thysanophrys celebicus*** (Bleeker, 1854)
Rare. Recorded in Australia only from Decapolis Reef (14°52'S) by Paxton et al. (1989: 472). Southern record QMI29809 from Curtin Artificial Reef. Tropical Indo-west Pacific.

***Thysanophrys cirronasus*** (Richardson, 1848)
Rare. Sight records from Amity Pt and Southport seaway only. Several closely related species are difficult to distinguish underwater and a specimen is required for confirmation. Reported north to Caloundra (Paxton et al., 1989: 472). Temperate eastern and southwestern Australia.

## DACTYLOPTERIDAE

***Dactyloptena orientalis*** (Cuvier, 1829)
Common. Tropical central and Indo-west Pacific.

***Dactyloptena papilio*** Ogilby, 1910
Common. Reported south to Moreton Bay by Paxton et al. (1989: 481). Extends south to off Port Stephens (32°12'S), AMSI24767-001 and Newcastle (33°00'S, Graham & Wood, 1997). Tropical Australia.

## CENTROPOMIDAE

***Psammoperca waigiensis*** (Cuvier, 1828)
Rare. Recorded south to Townsville by Paxton et al. (1989: 483). Common to Hervey Bay (25°17'S). Southern record QMI2611. Tropical east Indo-west Pacific.

## AMBASSIDAE

***Ambassis jacksoniensis*** Macleay, 1881
Common. Reported north to Moreton Bay by Allen and Burgess (1990). QM records extend to Burnett River (24°46'S, QMI23860). Temperate to subtropical eastern Australia.

***Ambassis marianus*** Günther, 1880
Abundant. Temperate to subtropical eastern Australia.

## SERRANIDAE

***Acanthistius ocellatus*** (Günther, 1859)
Rare. Voucher QMI3839. Northern limit. Temperate eastern Australia.

***Centrogenys vaigiensis*** (Quoy & Gaimard, 1824)
Common. Southern record QMI29867 from Myora. Tropical Indo-west Pacific.

***Cephalopholis boenack*** (Bloch, 1790)
Rare. Reported south to One Tree I. by Paxton et al. (1989: 491). Southern record QMI12193 from Myora. Tropical Indo-west Pacific.

***Cephalopholis miniatus*** (Forsskål, 1775)
Rare. Sight record from Southport seaway only. Reported south to One Tree I. (23°30'S) by Paxton et al., 1989: 491. Southern record. Tropical central and Indo-west Pacific.

***Cromileptes altivelis*** (Valenciennes, 1828)
Rare. Small juveniles reported south to Sydney by Kuiter (1993) but adults uncommon south of Bunker Group (24°00'S). Tropical Indo-west Pacific.

***Epinephelus coioides*** (Hamilton, 1822)
Abundant. The name *E. tauvina* (Forsskål, 1775) has often been incorrectly applied to this species, as well as to *E. malabaricus* (Paxton et al., 1989: 498). *E. tauvina* is known from Flinders Reef (26°58'S), QMI17426 and Point Lookout (27°26'S), QMI31308. However it is comparatively rare in the region and due to the absence of voucher specimens, all records of *E. tauvina* from Moreton Bay are treated as misidentifications of either *E. coioides* or *E. malabaricus*. Tropical Indo-west Pacific.

***Epinephelus cyanopodus*** (Richardson, 1846)
Uncommon inside Moreton Bay. Tropical east Indo-west Pacific.

***Epinephelus fasciatus*** (Forsskål, 1775)
Common. Tropical central and Indo-west Pacific.

***Epinephelus daemelii*** (Günther, 1876)
Rare inside Moreton Bay. Reported north to southern Qld (Paxton et al., 1989: 494; Heemstra & Randall, 1993) and to Townsville (19°16'S) by Hutchins & Swainston (1986: 52). Northernmost QM record confirmed from photographs of a large specimen taken off Breaksea Spit, Fraser I. (24°15'S) by A. Munn (Qld Boating & Fisheries Patrol) in 1998. Warm temperate to subtropical southwest Pacific.

***Epinephelus lanceolatus*** (Bloch, 1790)
Common. Tropical Indo-west Pacific.

***Epinephelus maculatus*** (Bloch, 1790)
Uncommon. Sight records of juveniles from Comboyuro Pt and Southport seaway only. Tropical central to west Pacific.

***Epinephelus malabaricus*** (Bloch & Schneider, 1801)
Common. Often confused with *E. coioides*. Tropical Indo-west Pacific.

***Epinephelus quoyanus*** (Valenciennes, 1830)
Uncommon inside Moreton Bay. Frequently confused with *E. merra* Bloch, 1793. The record of *E. merra* by McCulloch & Whitley (1925) cannot be verified and is treated as a misidentification. Tropical Indo-west Pacific.

***Epinephelus rivulatus*** (Valenciennes, 1830)
Rare inside Moreton Bay. Only record is from holotype of *E. viridipinnis* De Vis, 1884. Occurs north to Flinders Reef (26°58'S), QMI19184. Subtropical eastern and Western Australia, tropical central and Indo-west Pacific.

***Epinephelus sexfasciatus*** (Kuhl & van Hasselt, 1828)
Rare. Southern record QMI15129, from Deception Bay. Tropical east Indo-west Pacific.

***Epinephelus undulostriatus*** (Peters, 1867)
Common. Subtropical eastern Australia.

***Hypoplectrodes annulatus*** (Günther, 1859)
Doubtful record. Reported by Paxton et al. (1989: 504) north to Moreton Bay. Occasionally taken in deeper water (50-100m) north to Barwon Banks (26°40'S, QMI17873) but no records from inside Moreton Bay. Temperate eastern Australia.

***Hypoplectrodes jamiesoni*** Ogilby, 1908
Common. Temperate to subtropical eastern Australia.

***Hypoplectrodes maccullochi*** (Whitley, 1929)
Rare. Common off Southport and Cook Is. (28°12'S) but only one specimen from Moreton Bay. Northern record QMI31331 from Amity Pt. Temperate eastern Australia.

***Plectropomus leopardus*** (Lacepède, 1802)
Uncommon. Reported south to Lamont Reef by Paxton et al. (1989: 500). Several sightings at Curtin Artificial Reef and Tangalooma Wrecks only. Southern limit. Tropical Indo-west Pacific.

***Rainfordia opercularis*** McCulloch, 1923
Rare. Reported south to One Tree I. by Paxton et al. (1989: 500). Southern record QMI29166 from Tangalooma Wrecks, excluding Lord Howe I. (Francis, 1993). Tropical eastern and western Australia.

## PERCICHTHYIDAE

***Macquaria novemaculeata*** (Steindachner, 1866)
Common. Occasionally netted near mouths of Pine and Caboolture Rivers but more frequently reported from upper reaches, in or near freshwater. Temperate eastern Australia.

GRAMMISTIDAE

***Diploprion bifasciatum*** Kuhl & van Hasselt, 1828
Common. Tropical east Indo-west Pacific.

***Grammistes sexlineatus*** (Thunberg, 1792)
Rare. Reported south to Lizard I. (14°40'S) by Paxton et al. (1989: 517). Specimen from Comboyuro Pt, QMI30821 and a sight record from Myora. Recorded south to Palm Beach Reef (28°07'S), QMI19744 and Lord Howe I. (Francis, 1993). Tropical Indo-west Pacific.

PSEUDOCHROMIDAE

***Ogilbyina novaehollandiae*** (Steindachner, 1880)
Uncommon inside Moreton Bay. Reported south to Capricorn Group by Paxton et al. (1989: 519). Southern record QMI29158 from Tangalooma Wrecks. Subtropical to tropical eastern Australia.

***Pseudochromis cyanotaenia*** Bleeker, 1857
Rare. Only records QMI29863 and QMI30388 from Myora. Occurs south to Cook Is., NSW (28°12'S, QMI21711). Tropical east Indo-west Pacific.

***Pseudochromis fuscus*** Müller & Troschel, 1849
Rare. Only record QMI784, holotype of *P. wildii* Ogilby, 1908. Southern limit. Tropical east Indo-west Pacific.

PLESIOPIDAE

***Paraplesiops poweri*** Ogilby, 1908
Common. Subtropical eastern Australia.

***Plesiops corallicola*** Bleeker, 1853
Doubtful record. Known from Cocos-Keeling Is., northeastern Papua New Guinea and the Solomon Islands but not recorded from Australian coastal waters (Mooi, 1995). One specimen, QMI581 registered by Ogilby in 1912. Collection data possibly erroneous. Tropical central and east Indo-west Pacific.

***Plesiops genaricus*** Mooi & Randall, 1991
Rare. Reported south to Capricorn Group (Mooi, 1995). Southern record QMI31165 from Southport seaway. Tropical eastern Australia.

***Trachinops taeniatus*** Günther, 1861
Locally common at Curtin Artificial Reef, based on sightings only. Reported north to North Solitary Is., NSW by Paxton et al. (1989: 527). Extends to at least Mudjimba I. (26°37'S, QMI29094). Temperate eastern Australia.

ACANTHOCLINIDAE

***Belonepterygion fasciolatum*** (Ogilby, 1889)
Rare. Southern record QMI11241 from Myora, excluding Lord Howe I. (Francis, 1993). Tropical east Indo-west Pacific.

GLAUCOSOMATIDAE

***Glaucosoma scapulare*** Ramsay, 1881
Rare inside Moreton Bay. Commonly taken in depths of 40-150m outside Moreton Bay. Subtropical eastern Australia.

TERAPONTIDAE

***Amniataba caudavittata*** (Richardson, 1845)
Doubtful record. Reported south to Moreton Bay by Ogilby & McCulloch (1916) on the basis of an uncatalogued QM specimen which is no longer extant. QM records extend south to Sabina Pt (22°24'S, QMI28350). Tropical Australia and New Guinea.

***Helotes sexlineatus*** (Quoy & Gaimard, 1824)
Rare. Southern record QMI30884 from Manly (Fig. 2F). Tropical Australia.

***Pelates sexlineatus*** (Quoy & Gaimard, 1824)
Common near seagrass beds. References to *P. quadrilineatus* (Bloch, 1790) south of Hervey Bay may be misidentifications of this species. *Helotes sexlineatus* is similiar in colour, but is more elongate and has tricuspid teeth. Temperate to subtropical eastern Australia.

***Terapon jarbua*** (Forsskål, 1775)
Common. Tropical Indo-west Pacific.

***Terapon theraps*** (Cuvier, 1829)
Rare. Reported by Hyland (1988) from Brisbane R and J. Robins (unpubl. data) from Deception Bay. No specimens in QM. Reported south to Clarence R, NSW (29°26'S) (Graham & Wood, 1997). Tropical Indo-west Pacific.

KUHLIIDAE

***Kuhlia mugil*** (Forster, 1801)
Rare inside Moreton Bay. Sight record from Bulwer only. Tropical Indo-Pacific.

## PRIACANTHIDAE

***Priacanthus hamrur*** (Forsskål, 1775)
Uncommon inside Moreton Bay. Tropical Indo-west Pacific.

***Priacanthus macracanthus*** Cuvier, 1829
Common. Tropical to temperate east Indo-west Pacific.

## APOGONIDAE

***Apogon capricornis*** Allen & Randall, 1993
Uncommon. Tropical to subtropical eastern Australia.

***Apogon cavitiensis*** (Jordan & Seale, 1907)
Common. *Apogon virgulatus*, Allen & Randall, 1993 is a junior synonym (Allen & Randall, 1995). Previously misidentified as *A. hartzfeldii* Bleeker, 1852, a similiar species also known from eastern Australia. Tropical Indo-Australian Archipelago.

***Apogon cookii*** Macleay, 1881
Uncommon. Most reports from southern Qld are probably attributable to *A. limenus* Randall & Hoese. Tropical Indo-west Pacific.

***Apogon crassiceps*** Garman, 1903
Uncommon inside Moreton Bay. Characterised by elongate caudal peduncle with a vague dark midlateral longitudinal streak. Three cryptic species of red semitransparent *Apogon* have been collected in Moreton Bay. They are provisionally identified as *A. crassiceps, A. erythrinus* and *A. fuscus*; however these species and *A. coccineus* Rüppell, 1838 have been confused in the literature and require revision. Another similiar species, *A. doryssa* (Jordan & Seale), recognised by elongate second dorsal spine, is recorded from nearby Flinders Reef (26°59'S, QMI31177). Reported south to Pixie Reef (20°28'S) by Paxton et al. (1989: 546) and Lord Howe and Norfolk I. (Francis, 1993; Francis & Randall, 1993), however these may not be conspecific records. Most Australian records of *A. coccineus* probably refer to this species. Tropical central and east Indo-west Pacific.

***Apogon doederleini*** Jordan & Snyder, 1901
Uncommon. Tropical Indo-west Pacific.

***Apogon*** cf ***erythrinus*** Snyder, 1904
Rare. Characterised by rounded head and snout, deep body and stout caudal peduncle. One lot, QMI29156 from Tangalooma Wrecks. Southern record. Tropical Indo-west Pacific?

***Apogon fasciatus*** (White, 1790)
Abundant. Ranked second in abundance of trawled fishes from Moreton Bay by Stephenson & Burgess (1980). Tropical Indo-west Pacific.

***Apogon fraenatus*** Valenciennes, 1832
Rare. Sight record from Amity Pt only. Tropical central and Indo-west Pacific.

***Apogon fuscus*** Quoy & Gaimard, 1824
Rare. Similiar to *A. crassiceps* but has caudal peduncle and lower half of caudal fin dusky. Three lots, QMI29745, QMI30419 and QMI-31334 from Amity Pt. Southern record. Tropical Indo-west Pacific.

***Apogon limenus*** Randall & Hoese, 1988
Abundant. Subtropical eastern Australia.

***Apogon nigripinnis*** Cuvier, 1828
Common. Kuiter (1993) treated the eastern Australian form of this species as *A. atripes* (Ogilby, 1916). Tropical Indo-west Pacific.

***Apogon pallidofasciatus*** Allen, 1987
Uncommon. Reported from North West Cape to Broome, WA by Paxton et al. (1989: 550). Southern record QMI29873 from Myora. Tropical Australia.

***Apogon poecilopterus*** Cuvier, 1828
Common, in trawls. Reports of *A. ellioti* Day, 1875 by Stephenson & Burgess (1980) may be misidentifications of this species (*A. poecil-opterus* was not recorded in their surveys). *Apogon ellioti* is only known south to off Cliff Pt. (22°38'S, AMSI34360-001). Southern record QMI26163 from off Russell I. Tropical east Indo-west Pacific.

***Apogon semiornatus*** Peters, 1876
Uncommon inside Moreton Bay. Voucher QMI31153. Tropical Indo-west Pacific.

***Apogonichthys ocellatus*** Weber, 1913
Rare. Reported south to Capricorn Group (Paxton et al., 1989: 551). Southern record QMI31143 from Southport seaway. Tropical Indo-west Pacific.

***Foa brachygramma*** Jenkins, 1903
Uncommon. Record of *F. fo* Jordan & Seale, 1906 from Moreton Bay by Paxton et al. (1989: 554) is probably referable to this species. Allen (pers. comm., 1996) advised that most if not all Australian specimens of *Foa* are *F. brachygramma*. Southern record QMI30995 from Southport broadwater. Tropical central to east Indo-west Pacific.

***Fowleria variegata*** (Valenciennes, 1832)
Locally common at Amity Pt and Myora. Reported south to Capricorn Group by Paxton et al. (1989: 554) and Sydney Harbour by Kuiter (1993). Tropical Indo-west Pacific.

***Siphamia cuniceps*** Whitley, 1941
Uncommon. Temperate to subtropical eastern and western Australia.

***Siphamia rosiegaster*** (Ogilby, 1886)
Abundant. Temperate to subtropical eastern Australia.

SILLAGINIDAE

***Sillago analis*** Whitley, 1943
Common. Southern record QMI30977 from Brisbane R. Tropical Australia and southern New Guinea.

***Sillago ciliata*** Cuvier, 1829
Abundant. New Caledonia and eastern Australia.

***Sillago ingenuua*** McKay, 1985
Rare. Reported south to Adolphus Passage (10°38'S) by McKay (1992). Southern record QMI29546 (Fig. 2G) from Pearl Channel (27°06'S). Tropical east Indo-west Pacific.

***Sillago maculata*** Quoy & Gaimard, 1824
Abundant. Eastern Australia.

***Sillago robusta*** Stead, 1908
Common. Temperate to subtropical eastern and western Australia.

MALACANTHIDAE

***Malacanthus brevirostris*** Guichenot, 1848
Uncommon inside Moreton Bay. Sight records from Curtin Artificial Reef only. Tropical Indo-Pacific.

POMATOMIDAE

***Pomatomus saltatrix*** (Linnaeus, 1766)
Abundant. Temperate Atlantic and Indo-west Pacific.

ECHENEIDIDAE

***Echeneis naucrates*** Linnaeus, 1758
Common. Circumtropical.

***Remora remora*** Linnaeus, 1758
Uncommon inside Moreton Bay. Circumglobal.

CARANGIDAE

***Alectis ciliaris*** (Bloch, 1787)
Common. Circumtropical.

***Alectis indicus*** (Rüppell, 1830)
Common. Tropical Indo-west Pacific.

***Alepes*** sp.
Abundant. An undescribed species often confused with *A. djedaba* (Forsskål, 1775). Gunn (1990) considered '*A. apercna*' to be a probable nomen nudum inadvertently used by Grant (1987). Tropical Australia.

***Atule mate*** (Cuvier, 1833)
Uncommon. Voucher QMI26876. Reported south to Townsville by Paxton et al. (1989: 574) and Gunn (1990). Graham & Wood (1997) extended southern limit to Clarence River, NSW (29°26'S). Tropical central and Indo-west Pacific.

***Carangoides caeruleopinnatus*** (Rüppell, 1830)
Uncommon. Voucher QMI23423. Gunn (1990) recorded *C. diversa* (Whitley, 1940) and *C. uii* Wakiya, 1924 as junior synonyms and reported distribution as south to Townsville. Graham & Wood (1997) extended southern limit to Clarence River (29°26'S) and Newcastle (33°00'S), NSW. Tropical Indo-west Pacific.

***Carangoides chrysophrys*** (Cuvier, 1833)
Common. Tropical Indo-west Pacific.

***Carangoides dinema*** Bleeker, 1851
Rare. Widespread throughout the Indo-Pacific but reported to be absent from Australian waters by Gunn (1990). Closely related to *C. humerosus*, from which it differs in having a slightly lower soft dorsal ray count and a pale vs dusky spinous

dorsal fin. New record for Australia based on QMI22345, from Southport Broadwater. Tropical Indo-west Pacific.

***Carangoides ferdau*** (Forsskål, 1775)
Uncommon. Tropical central and Indo-west Pacific.

***Carangoides fulvoguttatus*** (Forsskål, 1775)
Locally common at Curtin Artificial Reef, from sight records of schools of large adults. Unconfirmed reports (Gunn, 1990) extended south to Solitary Islands, NSW (30°11'S). Tropical Indo-west Pacific.

***Carangoides humerosus*** (McCulloch, 1915)
Rare. Reported south to Bustard Head (24°08'S) by Gunn (1990). Southern record QMI30242 from off Shorncliffe (27°21'S). Tropical Australia and New Guinea.

***Carangoides malabaricus*** (Bloch & Schneider, 1831)
Common, in trawls. Southern limit extended from Moreton Bay to Clarence R. (29°26'S) and Newcastle (33°00'S), NSW by Graham & Wood (1997). Tropical Indo-west Pacific.

***Caranx ignobilis*** (Forsskål, 1775)
Common. Tropical central and Indo-west Pacific.

***Caranx melampygus*** Cuvier, 1833
Common. Tropical Indo-Pacific.

***Caranx papuensis*** Alleyne & Macleay, 1877
Rare. Reported south to Brisbane by Paxton et al. (1989: 578). No QM records from inside Moreton Bay, but one specimen, QMI31176 from Flat Rock (27°23'S). Southern record. Tropical central and Indo-west Pacific.

***Caranx sexfasciatus*** Quoy & Gaimard, 1825
Common. Tropical Indo-Pacific.

***Decapterus russelli*** (Rüppell, 1830)
Common. Reported south to Deception Bay (27°10'S) by Paxton et al. (1989: 580). Extends to Clarence River, NSW (29°23'S, AMSI-34108-001). Tropical Indo-west Pacific.

***Gnathanodon speciosus*** (Forsskål, 1775)
Common. Adults uncommon beyond Southport, juveniles occur south to Sydney (Kuiter, 1993). Tropical Indo-Pacific.

***Megalaspis cordyla*** (Linnaeus, 1758)
Uncommon inside Moreton Bay. Tropical Indo-west Pacific.

***Naucrates ductor*** (Linnaeus, 1758)
Uncommon inside Moreton Bay. Circumglobal.

***Parastromateus niger*** (Bloch, 1795)
Rare. Reported by Ogilby (1918b) from Coomera River. Paxton et al. (1989: 581) gave Townsville as southern limit. Southern record QMI3118. Tropical Indo-west Pacific.

***Pseudocaranx dentex*** (Bloch & Schneider, 1801)
Common. Temperate to subtropical Atlantic and central to Indo-west Pacific.

***Scomberoides commersonnianus*** Lacepède, 1801
Rare. One specimen, QMI29835 from Toorbul and a sight record from Southport. Reported from Tingalpa Ck mouth (Morton, 1990). Southern record. Tropical Indo-west Pacific.

***Scomberoides lysan*** (Forsskål, 1775)
Common. Tropical central and Indo-west Pacific.

***Scomberoides tol*** (Cuvier, 1832)
Uncommon. Reported south to Brisbane (Paxton et al. 1989: 583). Extends to Coolangatta (28°10'S, QMI5241). Tropical Indo-west Pacific.

***Selaroides leptolepis*** (Kuhl & van Hasselt, 1833)
Common. Southern limit extended from Moreton Bay to Clarence R. (29°26'S) by Graham & Wood (1997). Tropical Indo-west Pacific.

***Seriola dumerili*** (Risso, 1810)
Common. Temperate Atlantic and central to Indo-west Pacific.

***Seriola hippos*** Günther, 1876
Uncommon inside Moreton Bay. Temperate southwest Pacific and southwestern Australia.

***Seriola lalandi*** Valenciennes, 1833
Common. Temperate to subtropical circumglobal.

***Seriola rivoliana*** Valenciennes, 1833
Uncommon inside Moreton Bay. Sight records from Curtin Artificial Reef and Tangalooma Wrecks only. Regularly taken by anglers off Flinders Reef (26°58'S). Circumtropical.

***Seriolina nigrofasciata*** (Rüppell, 1829)
Uncommon. Reported south to Clarence R., NSW (29°26'S) by Graham & Wood (1997). Tropical Indo-west Pacific.

***Trachinotus anak*** Ogilby, 1909
Uncommon inside Moreton Bay. Tropical Australia and west Pacific.

***Trachinotus blochii*** (Lacepède, 1801)
Uncommon inside Moreton Bay. Tropical central and Indo-west Pacific.

***Trachinotus coppingeri*** (Günther, 1884)
Abundant. Subtropical eastern Australia.

***Trachurus declivis*** Jenyns, 1841
Common. Temperate to subtropical Australia and Southwest Pacific.

***Trachurus novaezelandiae*** Richardson, 1843
Common. Temperate to subtropical Australia and southwest Pacific.

***Ulua mentalis*** (Cuvier, 1833)
Rare. Reported south to Townsville (Paxton et al., 1989: 587). Southern record based on a sighting of a large specimen from Southport seaway. Tropical Indo-west Pacific.

***Uraspis uraspis*** (Gunther, 1860)
Rare. Southern record QMI10609. Tropical Indo-west Pacific.

CORYPHAENIDAE

***Coryphaena hippurus*** Linnaeus, 1758
Uncommon inside Moreton Bay. Circumtropical.

RACHYCENTRIDAE

***Rachycentron canadus*** (Linnaeus, 1766)
Common. Tropical Atlantic and central to Indo-west Pacific.

LEIOGNATHIDAE

***Leiognathus decorus*** (De Vis, 1884)
Common. Usually found in muddy upper reaches of mangrove creeks and estuaries. Reported south to Maryborough (25°32'S) by Jones (1985). Southern record QMI25332 from Pt Talburpin (27°39'S). Tropical Australia.

***Leiognathus moretoniensis*** (Ogilby, 1912)
Abundant. Ranked third in abundance of trawled fishes from Moreton Bay by Stephenson & Burgess (1980). Tropical to subtropical Australia.

LUTJANIDAE

***Lutjanus adetii*** (Castelnau, 1873)
Uncommon inside Moreton Bay. Tropical to subtropical eastern Australia to New Caledonia.

***Lutjanus argentimaculatus*** (Forsskål, 1775)
Common. Tropical Indo-west Pacific.

***Lutjanus carponotatus*** (Richardson, 1842)
Uncommon. Records from Tangalooma Wrecks, Curtin Artificial Reef and Comboyuro Pt. Tropical east Indo-west Pacific.

***Lutjanus fulviflamma*** (Forsskål, 1775)
Uncommon inside Moreton Bay. Sight records from Curtin Artificial Reef and Southport seaway only. Tropical Indo-west Pacific.

***Lutjanus gibbus*** (Forsskål, 1775)
Uncommon. Tropical Indo-west Pacific.

***Lutjanus kasmira*** (Forsskål, 1775)
Uncommon inside Moreton Bay. Tropical central and Indo-west Pacific.

***Lutjanus malabaricus*** Schneider, 1801
Uncommon. Tropical West Pacific to northern Indian Ocean.

***Lutjanus quinquelineatus*** (Bloch, 1790)
Uncommon. Tropical west Pacific to northern Indian Ocean.

***Lutjanus russelli*** (Bleeker, 1849)
Abundant. Tropical Indo-west Pacific.

***Lutjanus sebae*** (Cuvier, 1828)
Uncommon inside Moreton Bay. Tropical Indo-west Pacific.

***Lutjanus vitta*** (Quoy & Gaimard, 1824)
Uncommon. Southern record QMI17819 from Tangalooma Wrecks. Tropical Indo-west Pacific.

***Paracaesio xanthura*** (Bleeker, 1869)
Uncommon inside Moreton Bay. Subtropical to warm temperate eastern Australia and Indo-west Pacific.

***Pristipomoides filamentosus*** (Valenciennes, 1830)
Rare inside Moreton Bay. Common in deeper water outside the bay. Tropical central and Indo-west Pacific.

***Symphorus nematophorus*** (Bleeker, 1860)
Common. Usually found in this area as juveniles or subadults. Tropical western Pacific and Indo-Australian Archipelago.

CAESIONIDAE

***Caesio caerulaurea*** Lacepède, 1801
Uncommon inside Moreton Bay. Tropical Indo-west Pacific.

***Pterocaesio chrysozona*** (Cuvier, 1830)
Rare. A single specimen reported by Ogilby (1916b). No specimens in QM. Tropical Indo-west Pacific.

***Pterocaesio digramma*** (Bleeker, 1865)
Locally common at Tangalooma Wrecks, Curtin Artificial Reef and Comboyuro Pt. West Pacific and Indo-Australian Archipelago.

NEMIPTERIDAE

***Nemipterus hexodon*** (Quoy & Gaimard, 1824)
Uncommon. Southern limit QMI14777 from off Shorncliffe (27°20'S). Although not yet recorded, *N. theodorei* Ogilby, 1916 is commonly trawled to the east of Moreton Bay and is likely to occur in deeper areas near the East Channel. Tropical west Pacific and Indo-Australian Archipelago.

***Pentapodus paradiseus*** (Günther, 1859)
Abundant. Northeastern Australia and southern New Guinea to Solomon Is.

***Scolopsis bilineatus*** (Bloch, 1793)
Locally common at Comboyuro Pt, Amity Pt and Myora. Tropical east Indo-west Pacific.

***Scolopsis monogramma*** (Kuhl & Van Hasselt, 1830)
Common. Indo-Australian Archipelago and northwestern Pacific.

LOBOTIDAE

***Lobotes surinamensis*** (Bloch, 1790)
Uncommon. Circumtropical.

GERREIDAE

***Gerres filamentosus*** Cuvier, 1829
Rare. Southern record QMI3071. Tropical Indo-west Pacific.

***Gerres oyeana*** (Forsskål, 1775)
Common. Southern record QMI30321 from Dunwich. Tropical Indo-west Pacific.

***Gerres subfasciatus*** (Cuvier, 1830)
Abundant. Commonly used synonym *G. ovatus* Günther, 1859. Frequently confused with *G. oyeana*. Warm temperate to tropical Australia.

HAEMULIDAE

***Diagramma pictum labiosum*** Macleay, 1883
Common. Tropical to subtropical Australia and New Guinea.

***Plectorhinchus flavomaculatus*** (Ehrenberg, 1830)
Abundant. Tropical Indo-west Pacific.

***Plectorinchus gibbosus*** (Lacepède, 1802)
Common. Tropical Indo-west Pacific.

***Plectorhinchus lessoni*** (Cuvier, 1830)
Rare inside Moreton Bay. Frequently misidentified as *P. diagramma* (Linnaeus, 1758) and *P. lineatus* (*non* Linnaeus, 1758). Sight record of juvenile from Myora only. Tropical Indo-west Pacific.

***Plectorhinchus picus*** (Cuvier, 1830)
Rare inside Moreton Bay. Sight record of juvenile at Myora only. Tropical Indo-west Pacific.

***Plectorhinchus unicolor*** (Macleay, 1883)
Uncommon inside Moreton Bay. Previously misidentified as *P. schotaf* (Forsskål, 1775), a closely related species from the Indian Ocean and northwest Pacific. Tropical Australia and southern New Guinea.

***Pomadasys argenteus*** (Forsskål, 1775)
Uncommon. Tropical Indo-west Pacific.

***Pomadasys kaakan*** (Cuvier, 1830)
Uncommon. Anecdotal evidence suggests specimens to about 3 kg were commonly taken in Moreton Bay up to the 1960s. Southern record QMI19780 from Logan River. Tropical Indo-west Pacific.

***Pomadasys maculatum*** (Bloch, 1797)
Uncommon. Southern record QMI19779 from Logan River. Tropical Indo-west Pacific.

LETHRINIDAE

***Gymnocranius audleyi*** Ogilby, 1916
Uncommon inside Moreton Bay. Subtropical eastern Australia.

***Lethrinus genivittatus*** Valenciennes, 1830
Common. Frequently used synonym *L. nematacanthus* Bleeker, 1854. Western Pacific and Indo-Australian Archipelago.

***Lethrinus laticaudis*** Alleyne & Macleay, 1877
Common. Frequently used synonym *L. fletus* Whitley, 1943. Tropical Australia to southern Indonesia, Solomon Is. and New Caledonia.

***Lethrinus miniatus*** (Schneider, 1801)
Rare inside Moreton Bay. *Lethrinus chrysostomus* Richardson, 1848 is a junior synonym. *Lethrinus miniatus* had been previously misapplied to *L. olivaceus* Valenciennes, 1830 (Carpenter & Allen, 1989). Tropical Australia and New Caledonia.

***Lethrinus nebulosus*** (Forsskål, 1775)
Common. Tropical Indo-west Pacific.

SPARIDAE

***Acanthopagrus australis*** (Owen, 1853)
Abundant. Eastern Australia.

***Argyrops spinifer*** (Forsskål, 1775)
Uncommon. Tropical Indo-west Pacific.

***Pagrus auratus*** Schneider, 1801
Abundant. Temperate to subtropical Australia, southwest and northwest Pacific.

***Rhabdosargus sarba*** (Forsskål, 1775)
Common. Warm temperate and subtropical Indo-west Pacific.

SCIAENIDAE

***Argyrosomus japonicus*** (Temminck & Schlegel, 1843)
Common. Previously misidentified as *A. hololepidotus* (Lacepède, 1802), a species found by Griffiths & Heemstra (1995) to be endemic to Madagascar. Temperate to subtropical Indo-west Pacific.

***Johnius novaehollandiae*** (Steindachner, 1866)
Rare. Known from six specimens collected in the Logan and Brisbane Rivers. Trewavas (1977) implied that this species and *J. weberi* Hardenberg, 1936 may be synonymous and placed *Pseudomycterus maccullochi* Ogilby, 1908 (QMI1535 from Logan R.) in the synonymy of *J. belangerii* (Cuvier, 1830). She failed to examine the types of either *J. novaehollandiae* or *P. maccullochi*. Despite the availability of numerous specimens of this complex from Queensland waters, none are identifiable as *J. belangeri* using characters employed by Trevawas. Determinations of QM specimens made subsequently by K. Sasaki (pers. comm., 1993) are followed and both *P. maccullochi* and *J. weberi* are considered to be synonyms of *J. novaehollandiae*. Southern record (type locality of Port Jackson highly doubtful; type was despatched to Naturhistorisches Museum in Vienna from Sydney but was probably collected in Qld). Northeast Australia and Indo-Malay Archipelago?

***Johnius vogleri*** (Bleeker, 1853)
Abundant. Tropical east Indian Ocean and Indo-Australian Archipelago.

***Nibea soldado*** (Lacepède, 1802)
Rare. Reported by Ogilby (1918a). Southern record QMI3173. Tropical east Indian Ocean and Indo-Australian Archipelago.

MULLIDAE

***Mulloidichthys flavolineatus*** (Lacepède, 1801)
Common. Tropical central and Indo-west Pacific.

***Parupeneus ciliatus*** (Lacepède, 1801)
Locally common at Southport seaway and Amity Pt. Frequently confused with *P. spilurus*. Tropical central and Indo-west Pacific.

***Parupeneus heptacanthus*** (Lacepède, 1801)
Rare. One specimen, QMI31001 from Curtin Artificial Reef. Southern record, excluding Lord Howe I. (Francis, 1993). Tropical Indo-west Pacific.

***Parupeneus indicus*** (Shaw, 1803)
Rare. Sight records from Comboyuro Pt and Southport seaway only. Southern record. Tropical Indo-west Pacific.

***Parupeneus multifasciatus***
(Quoy & Gaimard, 1825)
Locally common at Comboyuro Pt and Curtin Artificial Reef. Voucher QMI29796. Tropical central and east Indo-west Pacific.

***Parupeneus spilurus*** (Bleeker, 1854)
Common. *Parupeneus signatus* (Günther, 1867) is generally considered synonymous (Randall et al., 1990). Kuiter (1993) treats *P. spilurus* as a species from Chinese and Japanese seas and *P. signatus* as a distinct Australian species. Subtropical eastern and western Australia and southwest Pacific.

***Upeneus tragula*** Richardson, 1846
Abundant. Tropical Indo-west Pacific.

MONODACTYLIDAE

***Monodactylus argenteus*** (Linnaeus, 1758)
Abundant. Tropical Indo-west Pacific.

***Schuetta scalaripinnis*** Steindachner, 1866
Locally common at Tangalooma Wrecks, Curtin Artificial Reef and Southport seaway. Temperate to subtropical eastern Australia.

PEMPHERIDAE

***Parapriacanthus ransonneti*** Steindachner, 1870
Rare. Sight record from Amity Pt only. Tropical Indo-west Pacific.

***Pempheris affinis*** McCulloch, 1911
Locally common at Curtin Artificial Reef. Sight records only. Temperate to subtropical eastern Australia.

***Pempheris schwenkii*** Bleeker, 1855
Common. Southern record QMI31164 from Southport seaway. Tropical Indo-west Pacific.

***Pempheris ypsilychnus*** Mooi & Jubb, 1996
Common. Southern record QMI30438 from Amity Pt. Tropical Australia.

LEPTOBRAMIDAE

***Leptobrama muelleri*** Steindachner, 1879
Rare. Two specimens, QMI1015 and AMSI12810 only. Ogilby (1913) recorded three females, 206 to 266mm, from Moreton Bay. Common north from Mary R. (25°30'S) Southern record. Tropical Australia and New Guinea.

KYPHOSIDAE

***Kyphosus bigibbus*** (Lacepède, 1803)
Common. Tropical to temperate central to Indo-west Pacific.

***Kyphosus cinerascens*** (Forsskål, 1775)
Common. Tropical Indo-west Pacific.

***Kyphosus sydneyanus*** (Günther, 1866)
Common. Temperate to subtropical Australia and southwest Pacific.

***Kyphosus vaigiensis*** (Quoy & Gaimard, 1825)
Common. Sasaki and Nakabo (1995) recognise *K. gibsoni* Ogilby, 1912 as a junior synonym. Tropical central to Indo-west Pacific.

GIRELLIDAE

***Girella elevata*** Macleay, 1881
Rare inside Moreton Bay. Only record QMI19589. Occasional reports from Pt Lookout and Cape Moreton. Recorded north to Caloundra (26°48'S, QMI12070). Temperate eastern Australia.

***Girella tricuspidata*** (Quoy & Gaimard, 1824)
Abundant. Temperate southeastern Australia and southwest Pacific.

SCORPIDIDAE

***Atypichthys strigatus*** (Günther, 1860)
Common. Occurs north to at least Fraser I. (25°13'S, personal observations, 1995). Temperate eastern Australia.

***Microcanthus strigatus*** (Langsdorff, 1831)
Abundant. Temperate to subtropical eastern and western Australia, central and west Pacific.

***Scorpis lineolatus*** Kner, 1865
Common. Occurs north to at least Fraser I. (25°13'S, personal observations, 1995).

Temperate eastern Australia and southwest Pacific.

EPHIPPIDIDAE

***Drepane punctata*** (Linnaeus, 1758)
Rare. Southern record QMI2614. Tropical Indo-west Pacific.

***Platax orbicularis*** (Forsskål, 1775)
Rare. Only record QMI11610. Tropical central and Indo-west Pacific.

***Platax teira*** (Forsskål, 1775)
Common. Tropical to warm temperate Indo-west Pacific.

SCATOPHAGIDAE

***Scatophagus argus*** (Linnaeus, 1766)
Common. Tropical Indo-west Pacific.

***Selenotoca multifasciata*** (Richardson, 1846)
Abundant. Tropical to subtropical Indo-Australian Archipelago.

CHAETODONTIDAE

***Chaetodon aureofasciatus*** Macleay, 1878
Uncommon. Tropical Australia and New Guinea.

***Chaetodon auriga*** Forsskål, 1775
Common. Tropical to warm temperate Indo-west Pacific.

***Chaetodon bennetti*** Cuvier, 1831
Rare. One specimen, QMI10529 and several sight records from the Myora area. Southern record, excluding Lord Howe I. (Francis, 1993). Tropical Indo-west Pacific.

***Chaetodon citrinellus*** Cuvier, 1831
Common. Tropical central and Indo-west Pacific.

***Chaetodon ephippium*** Cuvier, 1831
Common. Tropical central to east Indo-west Pacific.

***Chaetodon flavirostris*** Günther, 1873
Abundant. Tropical south Pacific.

***Chaetodon guentheri*** Ahl, 1913
Uncommon. Subtropical to temperate western Pacific.

***Chaetodon kleinii*** Bloch, 1790
Common. Tropical central and Indo-west Pacific.

***Chaetodon lineolatus*** Cuvier, 1831
Uncommon. Sight records from Myora and Southport seaway only. Tropical Indo-west Pacific.

***Chaetodon lunula*** (Lacepède, 1803)
Common. Tropical Indo-west Pacific.

***Chaetodon melannotus*** Bloch & Schneider, 1801
Uncommon. Tropical Indo-west Pacific.

***Chaetodon mertensii*** Cuvier, 1831
Uncommon. Tropical west Pacific.

***Chaetodon pelewensis*** Kner, 1868
Rare. Sight records from Myora only. Tropical south Pacific.

***Chaetodon plebeius*** Cuvier,1831
Locally common at Myora. Tropical east Indo-west Pacific.

***Chaetodon rafflesi*** Bennett, 1830
Rare. Sight records from Myora only. Tropical east Indo-west Pacific.

***Chaetodon rainfordi*** McCulloch, 1923
Locally common at Myora. Tropical eastern Australia.

***Chaetodon speculum*** Cuvier, 1831
Juveniles locally common at Myora. Tropical east Indo-west Pacific.

***Chaetodon trifasciatus*** Park, 1797
Locally common at Myora. Tropical central and Indo-west Pacific.

***Chaetodon ulietensis*** Cuvier, 1831
Uncommon. Tropical east Indo-west Pacific.

***Chaetodon unimaculatus*** Bloch, 1787
Uncommon. Sight records from Myora only. Tropical Indo-west Pacific.

***Chaetodon vagabundus*** Linnaeus, 1758
Common. Tropical Indo-west Pacific.

***Chelmon rostratus*** (Linnaeus, 1758)
Common. Tropical east Indo-west Pacific.

***Chelmonops truncatus*** (Kner, 1859)
Common. Temperate to subtropical eastern Australia.

***Coradion altivelis*** McCulloch, 1916
Common. Tropical west Pacific.

***Forcipiger flavissimus*** Jordan & McGregor, 1898
Rare. Two specimens from Myora, QMI1774 and QMI30380. Tropical Indo-Pacific.

***Heniochus acuminatus*** (Linnaeus, 1758)
Common. Tropical Indo-west Pacific.

***Heniochus monoceros*** Cuvier, 1831
Uncommon. Two specimens (AMI17270-001, QMI30425) and several sight records, all from Amity Pt. Tropical Indo-west Pacific.

***Parachaetodon ocellatus*** (Cuvier, 1831)
Common. Tropical east Indo-west Pacific.

POMACANTHIDAE

***Centropyge bicolor*** (Bloch, 1787)
Rare inside Moreton Bay. Only records QMI-1840-1 and several sight records from Myora area. Tropical east Indo-west Pacific.

***Centropyge bispinosus*** (Günther, 1860)
Rare inside Moreton Bay. Sight records from Myora and Amity Pt only. Tropical Indo-west Pacific.

***Centropyge tibicen*** (Cuvier, 1831)
Common. Records from Amity Pt, Myora and Southport seaway. Tropical east Indo-west Pacific.

***Centropyge vroliki*** (Bleeker, 1853)
Uncommon. Sight records from Amity Pt, Myora and Southport seaway. Tropical east Indo-west Pacific.

***Chaetodontoplus conspicillatus*** (Waite, 1900)
Rare. Sight record from Amity Pt only. Subtropical to tropical southwest Pacific.

***Chaetodontoplus duboulayi*** (Günther, 1867)
Rare. Reported by Ogilby (1915) and Marshall (1964). A recent sight record from Myora. Southern limit. Tropical Australia and New Guinea.

***Chaetodontoplus meredithi*** Kuiter, 1990
Uncommon. Tropical eastern Australia.

***Pomacanthus imperator*** (Bloch, 1787)
Rare inside Moreton Bay. One specimen, QMI30824 from Comboyuro Pt. Tropical Indo-west Pacific.

***Pomacanthus semicirculatus*** (Cuvier, 1831)
Common. Sight records from Tangalooma Wrecks, Amity Pt, Myora and Southport seaway. Tropical Indo-west Pacific.

***Pygoplites diacanthus*** (Boddaert, 1772)
Rare. Sight records from Amity Pt and Myora only. Tropical Indo-west Pacific.

ENOPLOSIDAE

***Enoplosus armatus*** (White, 1790)
Uncommon. Occurs north to Wide Bay (Gomon et al., 1994: 628). Southern Australia.

PENTACEROTIDAE

***Paristiopterus labiosus*** (Günther, 1871)
Rare. Recorded from off Manly, QMI20959 and Dunwich, QMI30883. Occurs north to Mooloolaba (26°40'S), QMI21274. Temperate southwest Pacific.

POMACENTRIDAE

***Abudefduf bengalensis*** (Bloch, 1787)
Abundant. Tropical east Indo-west Pacific.

***Abudefduf sexfasciatus*** (Lacepède, 1801)
Common. Tropical Indo-west Pacific.

***Abudefduf sordidus*** (Forsskål, 1775)
Uncommon inside Moreton Bay. Sight records from Bulwer only. Tropical Indo-west Pacific.

***Abudefduf vaigiensis*** (Quoy & Gaimard, 1825)
Common. Tropical Indo-west Pacific.

***Abudefduf whitleyi*** Allen & Robertson, 1974
Common. Tropical southwest Pacific.

***Amphiprion akindynos*** Allen, 1972
Common. Tropical southwest Pacific.

***Amphiprion latezonatus*** Waite, 1900
Rare inside Moreton Bay. Only record AMSI-17327-001. Northern limit. Northern NSW and southern Qld to Norfolk I.

***Chromis hypsilepis*** (Günther, 1876)
Uncommon. Reported north to Solitary Is., NSW by Gomon et al. (1994: 669). Sight records from Amity Pt and Southport seaway. Northern record. Temperate to subtropical southwest Pacific.

***Chromis margaritifer*** Fowler, 1946
Rare inside Moreton Bay. Only record QMI-31147 from Southport seaway. Tropical east Indo-west Pacific.

***Chromis nitida*** (Whitley, 1928)
Uncommon inside Moreton Bay. Sight records from Amity Pt and Southport seaway. Warm temperate to tropical southwest Pacific.

***Chromis viridis*** (Cuvier, 1830)
Rare. Only record QMI4490. Southern limit. Tropical Indo-west Pacific.

***Chrysiptera cyanea*** (Quoy & Gaimard, 1824)
Rare inside Moreton Bay. Several specimens, QMI10509, QMI30395 and AMSI21710-001. Southern limit. Tropical western Pacific to Indonesia.

***Chrysiptera*** cf ***flavipinnis*** (Allen & Robertson, 1974)
Uncommon. Two specimens from Myora, QMI29890, were tentatively identified by G.R. Allen. They lack the typical yellow colouration on the upper back and dorsal fin. Tropical southwest Pacific.

***Chrysiptera taupou*** (Jordan & Seale, 1906)
Rare inside Moreton Bay. Sight record from Amity Pt only. Southern record. Tropical southwest Pacific.

***Dascyllus aruanus*** (Linnaeus, 1758)
Rare inside Moreton Bay. Sight records from Myora only. Tropical Indo-west Pacific.

***Dascyllus melanurus*** Bleeker, 1854
Rare. Specimen from Peel I., QMI8993 and a sight record from Myora. Southern record. Tropical eastern Australia, Coral Sea and Indo-Malay Archipelago.

***Dascyllus trimaculatus*** (Rüppell, 1828)
Locally common at Curtin Artificial Reef and Myora. Voucher QMI29864. Tropical Indo-west Pacific.

***Dischistodus fasciatus*** (Cuvier, 1830)
Rare. Only record QMI2189, collected in 1914 and originally identified by G.P. Whitley. Southern limit. Tropical western Australia to Philippines.

***Mecaenichthys immaculatus*** (Ogilby, 1885)
Rare. Sight record from Amity Pt only. Occurs north to off Mooloolaba (26°40'S, QMI31320). Temperate to subtropical eastern Australia.

***Neopomacentrus bankieri*** (Richardson, 1845)
Abundant. Tropical eastern Australia and Indo-Malay Archipelago.

***Neopomacentrus cyanomos*** (Bleeker, 1856)
Uncommon. Tropical Indo-west Pacific.

***Parma oligolepis*** Whitley, 1929
Abundant. Warm temperate to tropical eastern Australia.

***Parma polylepis*** Günther, 1862
Rare. Sight record from Amity Pt only. Subtropical southwest Pacific.

***Parma unifasciata*** (Steindachner, 1867)
Common. Sight records from Comboyuro Pt, Bulwer, Amity Pt and Southport seaway. Temperate to subtropical eastern Australia.

***Plectroglyphidodon leucozonus*** (Bleeker, 1859)
Locally common at Southport seaway. Tropical Indo-west Pacific.

***Pomacentrus amboinensis*** Bleeker, 1868
Common. Tropical east Indo-west Pacific.

***Pomacentrus australis*** Allen & Robertson, 1973
Abundant. Subtropical eastern Australia.

***Pomacentrus brachialis*** Cuvier, 1830
Uncommon. Two specimens from Amity Pt, QMI29754 and QMI30446. Southern record. Tropical southwest Pacific and Indo-Australian Archipelago.

***Pomacentrus coelestis*** Jordan & Starks, 1901
Common. Tropical east Indo-west Pacific.

***Pomacentrus moluccensis*** Bleeker, 1853
Locally common at Amity Pt and Myora. Tropical east Indo-west Pacific.

***Pomacentrus nagasakiensis*** Tanaka, 1909
Locally common at Amity Pt, Myora and Southport seaway. Tropical east Indo-west Pacific.

***Pomacentrus wardi*** Whitley, 1927
Common. Tropical to subtropical eastern Australia.

***Stegastes apicalis*** (De Vis, 1885)
Common. Tropical eastern Australia.

***Stegastes gascoynei*** (Whitley, 1964)
Locally common at Amity Pt and Southport seaway. Tropical to warm temperate eastern Australia and southwest Pacific.

CIRRHITIDAE

***Cirrhitichthys aprinus*** (Cuvier, 1829)
Uncommon inside Moreton Bay. Specimen, QMI30261 and sight records from Amity Pt and sight records from Southport seaway. Tropical to subtropical Indo-Australian Archipelago.

***Cirrhitichthys falco*** Randall, 1963
Uncommon inside Moreton Bay. Specimen, QMI30349 from Myora and sight records from Amity Pt. Tropical eastern Australia and east Indo-west Pacific.

CHIRONEMIDAE

***Chironemus marmoratus*** Günther, 1860
Uncommon inside Moreton Bay. Sight records from Southport seaway only. Temperate southwest Pacific.

APLODACTYLIDAE

***Crinodus lophodon*** Günther, 1859
Locally common at Southport seaway but rare elsewhere in Moreton Bay. Northern record QMI12097 from off Bribie I. Temperate eastern Australia.

CHEILODACTYLIDAE

***Cheilodactylus fuscus*** Castelnau, 1879
Common. Reported by Ogilby (1908a). Sight records from Tangalooma Wrecks, Curtin Artificial Reef and Southport seaway. Temperate to subtropical eastern Australia to New Zealand.

***Cheilodactylus vestitus*** (Castelnau, 1878)
Abundant. Warm temperate to subtropical eastern Australia and southwest Pacific.

CEPOLIDAE

***Acanthocepola krusensternii*** Schlegel, 1850
Common. Erroneously recorded by Marshall (1925;1964) as *Cepola australis* Ogilby, 1899, a southern species that apparently does not reach this area. Fifteen specimens in QM, most taken by trawl. Occurs south to at least off Currumbin (28°08'S, QMI21722). Tropical east Indo-west Pacific.

MUGILIDAE

***Crenimugil crenilabis*** (Forsskål, 1775)
Rare. Only record that of *Mugil papillosa* Macleay, 1883 (Tosh, 1903; McCulloch & Whitley, 1925) which is almost certainly referable to this species. Known from nearby Flinders Reef (26°58'S), QMI28331. Tropical Indo-west Pacific.

***Liza argentea*** (Quoy & Gaimard, 1825)
Common. Temperate to subtropical Australia.

***Liza subviridis*** (Valenciennes, 1836)
Abundant. Tropical Indo-west Pacific.

***Mugil cephalus*** Linnaeus, 1758
Abundant. Temperate to tropical circumglobal.

***Myxus elongatus*** Günther, 1861
Common. Temperate to subtropical Australia and southwest Pacific.

***Valamugil georgii*** (Ogilby, 1897)
Abundant. Subtropical to tropical northeastern Australia.

***Valamugil seheli*** (Forsskål, 1775)
Rare. Reported south to Brisbane by Marshall (1951) but only to Bundaberg (24°45'S) by Grant (1987). One specimen in QM. Southern record QMI30250, excluding Norfolk I. (Francis, 1993). Tropical Indo-west Pacific.

SPHYRAENIDAE

***Sphyraena acutipinnis*** Day, 1876
Uncommon inside Moreton Bay. Tropical central and Indo-west Pacific.

***Sphyraena barracuda*** Walbaum, 1792
Common. Tropical central and Indo-west Pacific.

***Sphyraena flavicauda*** Ruppell, 1838
Common. Tropical central and Indo-west Pacific.

***Sphyraena jello*** Cuvier, 1829
Common. Tropical Indo-west Pacific.

***Sphyraena obtusata*** Cuvier, 1829
Abundant. Tropical central and Indo-west Pacific.

***Sphyraena putnamiae*** Jordan & Seale, 1905
Uncommon inside Moreton Bay. Tropical Indo-west Pacific.

POLYNEMIDAE

***Polydactylus multiradiatus*** (Günther, 1860)
Abundant. Tropical Indo-Australian Archipelago.

***Polydactylus sheridani*** (Macleay, 1884)
Uncommon. Occasionally taken by beam trawlers near Pine and Caboolture R. mouths, reportedly when banana prawns, *Peneus merguiensis* are schooled. Photograph sighted of a large specimen taken by S. Goleby from Brisbane R. in 1997. Only specimen QMI8042 from Toorbul (27°04'S). Southern record. Tropical northeastern Australia and southern New Guinea.

LABRIDAE

***Achoerodus viridis*** (Steindachner, 1866)
Uncommon inside Moreton Bay. Reported by McCulloch & Whitley (1926). Sight records from Amity Pt and Southport seaway. Southeastern Australia.

***Anampses caeruleopunctatus*** Rüppell, 1829
Uncommon. Sight records from Amity Pt and Southport seaway only. Tropical Indo-west Pacific.

***Anampses geographicus*** Valenciennes, 1840
Locally common at the Southport seaway. Tropical Australia and west Pacific.

***Bodianus perditio*** (Quoy & Gaimard, 1835)
Uncommon inside Moreton Bay. Subtropical southern Indian Ocean, southwest and northwest Pacific.

***Bodianus unimaculatus*** (Günther, 1862)
Rare inside Moreton Bay. Temperate to subtropical eastern Australia and southwest Pacific.

***Cheilinus chlorurus*** (Bloch, 1791)
Rare. One lot from Amity Pt, QMI30430. Southern record. Tropical central and Indo-west Pacific.

***Cheilinus trilobatus*** Lacepède, 1801
Uncommon. Sight records from Amity Pt and Southport seaway only. Southern record. Tropical central and Indo-west Pacific.

***Cheilio inermis*** (Forsskål, 1775)
Common. Tropical to subtropical central and Indo-west Pacific.

***Choerodon cephalotes*** (Castelnau, 1875)
Common. Tropical Indo-Australian Archipelago.

***Choerodon fasciatus*** (Günther, 1867)
Uncommon inside Moreton Bay. Subtropical to tropical eastern Australia, New Caledonia and northwest Pacific.

***Choerodon graphicus*** (De Vis, 1885)
Uncommon. Tropical eastern Australia and New Caledonia.

***Choerodon schoenleinii*** (Valenciennes, 1839)
Common. Tropical Australia and western Pacific.

***Choerodon venustus*** (De Vis, 1884)
Uncommon inside Moreton Bay. Subtropical to tropical eastern Australia.

***Cirrhilabrus punctatus*** Randall & Kuiter, 1989
Locally common at Amity Pt and Myora. Tropical to subtropical eastern Australia and southwest Pacific.

***Coris aurilineata*** Randall & Kuiter, 1982
Locally common at Comboyuro Pt, Amity Pt and Myora. Subtropical eastern Australia.

***Coris batuensis*** (Bleeker, 1856)
Locally common at Amity Pt and Myora. Tropical Indo-west Pacific.

***Coris picta*** (Bloch & Schneider, 1801)
Common. Temperate to subtropical eastern Australia and southwest Pacific.

***Halichoeres hartzfeldii*** (Bleeker, 1852)
Uncommon. Specimen, QMI11591 and sight records from Myora and Amity Pt. Tropical Indo-west Pacific.

***Halichoeres margaritaceus*** (Valenciennes, 1839)
Locally common at Bulwer and Amity Pt. Sight records only. Tropical to subtropical east Indo-west Pacific.

***Halichoeres marginatus*** Rüppell, 1835
Locally common at Amity Pt and Southport seaway. Tropical central and Indo-west Pacific.

***Halichoeres melanurus*** (Bleeker, 1851)
Uncommon. Sight records from Amity Pt only. Tropical western Pacific.

***Halichoeres nebulosus*** (Valenciennes, 1839)
Uncommon inside Moreton Bay. Sight records from Bulwer and Amity Pt only. Tropical to warm temperate Indo-west Pacific.

***Halichoeres trimaculatus*** (Quoy & Gaimard, 1834)
Common. Sight records from Myora and Amity Pt only. Tropical east Indo-west Pacific.

***Hemigymnus fasciatus*** (Bloch, 1792)
Uncommon. Specimen, AMSI17118-001 from Amity Pt. Juveniles sighted at Amity Pt and Myora. Tropical central and Indo-west Pacific.

***Hemigymnus melapterus*** (Bloch, 1791)
Adults uncommon inside Moreton Bay. Juveniles often sighted at Amity Pt. Voucher QMI29481 from Tangalooma Wrecks. Tropical Indo-west Pacific.

***Labroides dimidiatus*** (Valenciennes, 1839)
Common. Tropical to warm temperate central and Indo-west Pacific.

***Labropsis xanthonota*** Randall, 1981
Rare. Sight record from Myora only. Tropical eastern Australia and Indo-west Pacific.

***Notolabrus gymnogenis*** (Günther, 1862)
Locally common at Southport seaway. Rare elsewhere in Moreton Bay. Recorded north to Mooloolaba (Ogilby, 1908) and off Point Cartwright (personal observations, 1995). Temperate to subtropical eastern Australia.

***Ophthalmolepis lineolatus*** (Valenciennes, 1839)
Uncommon. Sight records from Amity Pt and Southport seaway only. Reported north to Byron Bay, NSW by Hutchins & Swainston (1986). Occurs north to at least Caloundra (26°48'S, QMI4376). Temperate to subtropical Australia.

***Oxycheilinus bimaculatus*** (Valenciennes, 1840)
Common. Tropical central and Indo-west Pacific.

***Pseudolabrus guentheri*** Bleeker, 1862
Abundant. Subtropical eastern Australia.

***Pterogogus cmeacanthus*** (Bleeker, 1852)
Uncommon. One specimen, QMI31137 and several sight records from Southport seaway. Tropical west Pacific and Indo-Australian Archipelago.

***Pterogogus flagellifera*** (Cuvier & Valenciennes, 1839)
Common. Tropical Indo-west Pacific.

***Stethojulis bandanensis*** (Bleeker, 1851)
Uncommon. Sight records from Amity Pt and Southport seaway only. Tropical Pacific.

***Stethojulis interrupta*** (Bleeker, 1851)
Common. Specimen from Myora, QMI30391 and sight records from Amity Pt and Southport seaway. Tropical Indo-west Pacific.

***Stethojulis strigiventer*** (Bennett, 1832)
Locally common at Amity Pt and Myora. Voucher QMI30390. Tropical Indo-west Pacific.

***Suezichthys gracilis*** (Steindachner & Döderlein, 1887)
Uncommon. Kuiter (1993) regards the Australian form of this species as *S. devisi* (Whitley, 1941). Sight records from Myora only. Subtropical northwest and southwest Pacific.

***Thalassoma amblycephalum*** (Bleeker, 1856)
Uncommon inside Moreton Bay. Sight records from Amity Pt and Southport seaway only. Tropical central and Indo-west Pacific.

***Thalassoma hardwicke*** (Bennett, 1828)
Locally common at Amity Pt. Tropical central and Indo-west Pacific.

***Thalassoma janseni***(Bleeker, 1856)
Common. Tropical east Indo-west Pacific.

***Thalassoma lunare*** (Linnaeus, 1758)
Abundant. Tropical central and Indo-west Pacific.

***Thalassoma lutescens*** (Lay & Bennett, 1839)
Common. Tropical Indo-Pacific.

***Thalassoma trilobatum*** (Lacepède, 1801)
Uncommon inside Moreton Bay. Sight records from Southport seaway and Bulwer only. Tropical central and Indo-west Pacific.

***Xyrichtys jacksoniensis*** (Ramsay, 1881)
Locally common off the north-western beaches of Moreton I., along sandy dropoffs. Subtropical eastern Australia.

ODACIDAE

***Odax cyanomelas*** (Richardson, 1850)
Rare. Usually found along rocky shores in surf zones. Reported by Ogilby (1908a) and Marshall (1964) as northern limit. Specimens confirmed north to Angourie Pt, NSW only (Gomon & Paxton, 1985). Temperate Australia.

SCARIDAE

***Calotomus carolinus*** (Valenciennes, 1840)
Rare. Reported from Moreton Bay by Marshall (1964: 320) as *Cryptotomus (= Calotomus) spinidens* (*non* Quoy & Gaimard, 1824). Bruce & Randall (1985) regard most prior references to *C. spinidens* as in error and applicable to *C. carolinus*. Unconfirmed sight record from Southport seaway. Tropical Indo-Pacific.

***Leptoscarus vaigiensis*** (Quoy & Gaimard, 1824)
Common. Tropical central and Indo-west Pacific.

***Scarus ghobban*** Forsskål, 1775
Abundant. Tropical Indo-Pacific.

***Scarus microrhinos*** Rüppell, 1828
Rare inside Moreton Bay. Sight record from Curtin Artificial Reef only. Tropical Australia, central and west Pacific.

OPISTOGNATHIDAE

***Opistognathus eximius*** (Ogilby, 1908)
Uncommon. Tropical to subtropical eastern Australia.

***Opistognathus jacksoniensis*** (Macleay, 1881)
Uncommon. Subtropical eastern Australia.

PINGUIPEDIDAE

***Parapercis cylindrica*** (Bloch, 1797)
Locally common at Amity Pt, Myora and Southport seaway. Tropical west Pacific.

***Parapercis diplospilus*** Gomon, 1981
Common. Tropical Indo-Australian Archipelago.

***Parapercis nebulosus*** (Quoy & Gaimard, 1825)
Abundant. Tropical Australia.

***Parapercis stricticeps*** (De Vis, 1884)
Common. Subtropical to tropical eastern Australia.

PERCOPHIDAE

***Matsubaraea fusiforme*** (Fowler, 1943)
Uncommon. Known from 12 specimens taken by small-meshed sled and dredge on the Western Banks, Moreton Bay (Fig. 2H). Found in 3 to 5m depth on subtidal sandbanks subject to wave break at low tide. Observations in captivity suggest this species is capable of rapidly burying in loose sandy substrate. Noichi et al. (1991) give a description of the depth distribution of *M. fusiforme* off a beach in Japan. Differs from closely related *Enigmapercis* Whitley by the presence of inward projecting cirri on the edge of the anterior nasal openings. Previously known from Japan, Philippines and the Gulf of Thailand (Matsuura, 1991). In Australia, specimens from Port Curtis, 23°55'S (AMIA4191) and Moreton Bay (QMI30689, QMI30692 and QMI30696). New record for Australia. Subtropical eastern Australia and northwest Pacific.

CREEDIIDAE

***Schizochirus insolens*** Waite, 1904
Rare. Records from Cowan Cowan, QMI4347 and Western Banks, QMI30698. Known only from a few specimens taken between Island Head (22°19'S, AMSI34384-010) and Maroubra Bay, NSW (Nelson, 1978). Subtropical eastern Australia.

LEPTOSCOPIDAE

***Lesueurina platycephala*** Fowler, 1907
Uncommon inside Moreton Bay. Reported (as *Leptoscopus macropygus* Richardson) north to Cape Moreton (27°02'S) by Ogilby (1912: 57). QM records extend north to Fraser I. (25°31'S, QMI31365). Temperate to subtropical Australia.

URANOSCOPIDAE

***Ichthyscopus sannio*** Whitley, 1936
Common. Subtropical eastern Australia.

***Ichthyscopus nigripinnis*** (Gomon & Johnson, 1999)
Uncommon. Voucher QMI30217. Subtropical eastern Australia to southern New Guinea.

BLENNIDAE

***Istiblennius edentulus*** (Schneider, 1801)
Rare inside Moreton Bay. Only record QMI29672 from Woody Pt (27°16'S). Tropical central and Indo-west Pacific.

***Istiblennius meleagris*** (Valenciennes, 1836)
Abundant. Subtropical to tropical Australia.

***Laiphognathus*** cf ***multimaculatus*** Smith, 1955
Common. Springer (1972;1981) reported *L. multimaculatus* from East Africa to the Solomon Islands, with Australian records limited to Kendrew I., WA. Specimens examined from eastern Australia, especially those from central Qld to northern NSW (Fig. 2I), differ from *L. multimaculatus* (Smith 1959, pl. 17, fig. 2) in colour and are considerably more elongate. Known from False Orford Ness, Cape York (11°23'S, AMSI20776-046), south to Cook Is., NSW (28°12'S, QMI22147). Tropical eastern Australia?

***Meiacanthus lineatus*** (De Vis, 1884)
Locally common at Amity Pt and Myora. Tropical eastern Australia.

***Omobranchus anolius*** (Valenciennes, 1836)
Common. Central South Australia and eastern Australia.

***Omobranchus punctatus*** (Valenciennes, 1836)
Abundant. Tropical Indo-west Pacific.

***Omobranchus rotundiceps rotundiceps*** (Macleay, 1881)
Common. Subtropical to tropical Australia.

***Omobranchus verticalis*** Springer & Gomon, 1975
Rare. All Qld records between Moreton Bay and Cleveland Bay (19°18'S). Numerous disjunct records from Northern Territory, between western Gulf of Carpentaria and Darwin in the NTM. Usually found inside damp mangrove logs in the supralittoral zone. Southern record QMI25243 from Brisbane R. Northeastern Australia.

***Parablennius tasmanianus intermedius*** (Ogilby, 1915)
Abundant. Eastern Australia.

***Petroscirtes fallax*** Smith-Vaniz, 1976
Locally common at Amity Pt. Subtropical to tropical eastern Australia.

***Petroscirtes lupus*** (De Vis, 1886)
Abundant. Subtropical eastern Australia and southwest Pacific.

***Petroscirtes variabilis*** Cantor, 1850
Common. Tropical eastern Australia and Indo-Malay Archipelago.

***Plagiotremus tapeinosoma*** (Bleeker, 1857)
Common. Tropical central and Indo-west Pacific.

***Plagiotremus rhinorhynchos*** (Bleeker, 1852)
Uncommon. Specimens QMI30436 and QMI31149 from Amity Pt, and sight records from Southport seaway. Tropical central and Indo-west Pacific.

***Xiphasia setifer*** Swainson, 1839
Common. Tropical Indo-west Pacific.

## TRIPTERYGIIDAE

***Enneapterygius atrogulare*** (Günther, 1873)
Common. Frequently used synonym *E. annulatus* (Ramsay & Ogilby, 1887). Eastern Australia.

***Enneapterygius hemimelas*** (Kner & Steindachner, 1866)
Rare inside Moreton Bay. Only record QMI-31166 from Southport seaway. Tropical Australia, Indonesia and western Pacific.

***Enneapterygius tutuilae*** Jordan & Seale, 1906
Uncommon. Reported south to Fairfax Reef (23°51'S) by Fricke (1994). Southern record QMI29245 from Tangalooma Wrecks. Tropical central and Indo-west Pacific.

***Lepidoblennius haplodactylus*** Steindachner, 1867
Rare or now absent. Only record QMI29671 from Redcliffe, collected in early 1900's. Type locality of Rockhampton represents only record north of Moreton Bay. Recent efforts unsuccessful in locating this species north of Fingal Head, NSW (28°12'S), QMI21550. Temperate eastern Australia.

***Norfolkia thomasi*** Whitley, 1964
Common. Reported south to Capricorn Group by Fricke (1994: 477). QM records extend to Byron Bay, NSW (28°38'S), QMI28161. Tropical Australia and west Pacific.

***Ucla xenogrammus*** Holleman, 1993
Rare. Reported south to Lady Musgrave I. (23°54'S) by Fricke (1994: 559). Southern record QMI29753 from Amity Pt. Tropical east Indo-west Pacific.

## CLINIDAE

***Cristiceps aurantiacus*** Castelnau, 1879
Uncommon. Two specimens from Southport in QM. Recent reports from the Southport seaway by aquarium fish collectors. Northern record QMI7514. Warm temperate eastern Australia and southwest Pacific.

***Heteroclinus*** sp.
Rare. One specimen, QMI10731. Undescribed species recognised by D. Hoese (pers. comm., 1996). Warm temperate eastern Australia.

***Peronedys anguillaris*** Steindachner, 1884
Doubtful record based on holotype of the synonymous *Scleropteryx devisi* (Ogilby, 1894) and followed by Marshall (1964). The type reported to be in QM (QMI362) according to McCulloch (1929-30), but two syntypes (AMI362) are in AMS. George & Springer (1980) report that the locality of capture is much further north than any other ophiclinin and may be erroneous. Eastern South Australia.

## AMMODYTIDAE

***Ammodytoides vaga*** (McCulloch & Waite, 1916)
Uncommon. Subtropical eastern Australia.

## CALLIONYMIDAE

***Callionymus belcheri*** Richardson, 1844
Common. Southern record QMI11049, from off Tangalooma. Northeastern Australia and southern New Guinea.

***Callionymus calcaratus*** Macleay, 1881
Common. Temperate to subtropical eastern and southwestern Australia and southwest Pacific.

***Callionymus grossi*** Ogilby, 1910
Common. Southern limit. Tropical Australia.

***Callionymus limiceps*** Ogilby, 1908
Abundant. Subtropical eastern Australia.

***Callionymus macdonaldi*** Ogilby, 1911
Abundant. Subtropical eastern Australia.

***Callionymus russelli*** Johnson, 1976
Common. Tropical eastern and northeastern Australia. Southern record CAS31863.

***Callionymus sublaevis*** McCulloch, 1926
Common. Southern record QMI10182 from off St Helena I. Tropical Australia.

***Dactylopus dactylopus*** (Valenciennes, 1837)
Uncommon. Specimens in AMS south to Brunswick Heads (28°33'S), NSW (M. McGrouther pers. comm., 1997). Tropical east Indo-west Pacific.

***Synchiropus ocellatus*** (Pallas, 1770)
Rare. Only record QMI29782 from Amity Pt. Tropical west Pacific.

GOBIIDAE
GOBIINAE

***Acentrogobius caninus*** (Cuvier & Valenciennes, 1837)
Common. Tropical Indo-west Pacific.

***Afurcagobius tamarensis*** (Johnston, 1883)
Rare. No specimens in QM. Previously placed in the genus *Favonigobius*. Reported by Young & Wadley (1979). Northern limit (D. Hoese pers. comm., 1996). Temperate Australia.

***Amblygobius phalaena*** (Valenciennes, 1837)
Common. Tropical to subtropical Indo-Pacific.

***Amoya*** sp.
Common. Identified as A. sp. 4 (Larson pers. comm., 1998). Five specimen lots in QM, QMI-13397, QMI30965, QMI31020, QMI31090 and QMI31178. Southern record from Nundah Ck. Subtropical eastern Australia.

***Arenigobius frenatus*** (Günther, 1861)
Abundant. Temperate to subtropical eastern Australia.

***Arenigobius leftwichi*** (Ogilby, 1910)
Uncommon. Voucher QMI13382. Tropical to subtropical eastern Australia.

***Austrolethops wardi*** Whitley, 1935
Rare. Vouchers QMI7400 and QMI31189 (Fig. 2J). Tropical Indo-Australian Archipelago and Indian Ocean.

***Bathygobius kreffti*** (Steindachner, 1866)
Abundant. Temperate to subtropical eastern Australia and South Australia.

***Bathygobius laddi*** (Fowler, 1931)
Uncommon inside Moreton Bay. Vouchers QMI-29531, QMI30237, QMI31161 and QMI31162. Tropical Indo-west Pacific.

***Calamiana*** sp.
Rare. Identified as *C.* sp. 2 (H. Larson pers. comm., 1998). Usually found in supralittoral and saltmarsh areas. Southern record QMI31278 from Eden I. (27°45'S). Tropical Australia.

***Callogobius depressus*** (Ramsay & Ogilby, 1886)
Rare. Voucher QMI29532. Temperate Australia.

***Callogobius*** sp.
Uncommon. An undescribed species referred to as *C.* sp. 6 (D. Hoese pers. comm., 1996). Specimens from Amity Pt, QMI29751; Myora, QMI29891 and QMI30364; and Southport seaway, QMI31141. Tropical to subtropical west Pacific.

***Coryphopterus neophytus*** (Günther, 1877)
Common. Previously placed in the genus *Fusigobius*. Specimens from Amity Pt, QMI29746, QMI30429 and QMI31345 and sight records from Southport seaway. Tropical central and Indo-west Pacific.

***Cristatogobius gobioides*** (Ogilby, 1886)
Common. Subtropical eastern Australia.

***Cryptocentrus*** sp.?
Common. May represent an undescribed genus and species (D. Hoese pers. comm., 1996). Recognised by vertical orange bars on head and 4 or 5 diffuse dusky blotches on sides. Observed at Myora occupying abandoned burrows of the mud lobster, *Neaxius glyptocercus* (von Martens). Voucher specimens, QMI17913, QMI29226 and QMI30961 (Fig. 2K). Subtropical eastern Australia.

***Drombus*** cf ***triangularis*** (Weber, 1911)
Common. Found in estuaries and littoral rocky reefs. Ten specimen lots in QM. Voucher QMI-27121. Tropical Indo-Australian Archipelago.

***Eviota*** cf ***melasma*** Lachner & Karnella, 1980
Rare. Only specimen QMI31132 from Southport seaway. Southern record. Tropical western Pacific.

***Favonigobius exquisitus*** Whitley, 1950
Abundant. Subtropical eastern Australia.

***Favonigobius lentiginosus*** (Richardson, 1844)
Abundant. Commonly referred to as *F. lateralis* Macleay, 1881, a species not occurring north of Victorian waters (D. Hoese pers. comm., 1996). Subtropical eastern Australia.

***Glossogobius biocellatus*** (Valenciennes, 1837)
Uncommon. Found in estuaries. Southern record QMI31080 from Southport broadwater. Tropical Indo-west Pacific.

***Gnatholepis*** sp.
Uncommon. Undescribed species currently under study by Randall and Greenfield. Usually found on rocky littoral reefs. Voucher QMI20350. Subtropical eastern Australia.

***Gobiodon quinquestrigatus*** (Valenciennes, 1837)
Rare. Only record QMI10973 from Myora. Tropical east Indo-west Pacific.

***Gobiopterus semivestita*** (Munro, 1949)
Abundant. South Australia to subtropical Qld.

***Istigobius decoratus*** (Herre, 1927)
Locally common at Amity Pt. Tropical Indo-west Pacific.

***Istigobius nigroocellatus*** (Günther, 1874)
Common. Tropical west Pacific and Indo-Australian Archipelago.

***Mugilogobius platynotus*** (Günther, 1861)
Rare. Voucher QMI31368. Northeastern Australia.

***Mugilogobius stigmaticus*** (De Vis, 1884)
Abundant. Northeastern Australia.

***Pandaka lidwilli*** (McCulloch, 1917)
Uncommon. Usually found in estuaries. Voucher QMI25244. Tropical west Pacific and Indo-Australian Archipelago.

***Parachaeturichthys polynema*** (Bleeker, 1853)
Common. Tropical Indo-west Pacific.

***Parkraemeria ornata*** Whitley, 1951
Uncommon. Only records QMI13368, QMI-31077 and AMSI19581-001. Tropical west Pacific.

***Priolepis cincta*** (Regan, 1908)
Uncommon. Specimen, QMI29168 from Tangalooma Wrecks and a sight record from Curtin Artificial Reef. Tropical Indo-west Pacific.

***Priolepis*** cf ***fallacincta*** Winterbottom & Burridge, 1992
Rare. Southern record QMI29805 from Curtin Artificial Reef. Tropical eastern Australia, Indo-Malay Archipelago and west Pacific.

***Priolepis nuchifasciata*** (Günther, 1873)
Common. Tropical to subtropical eastern Australia.

***Pseudogobius*** sp.
Abundant. Identified as *P.* sp. 2 (H. Larson pers. comm., 1998). Warm temperate to subtropical eastern Australia.

***Redigobius cf bikolanus*** (Herre, 1927)
Common. Tropical eastern Australia?

***Redigobius macrostomus*** (Günther, 1861)
Common. Temperate eastern Australia.

***Silhouettea*** cf ***evanida*** Larson & Miller, 1985
Uncommon? Small inconspicuous species found on subtidal bare sandy substrate. Southern record QMI30695 from Western Banks (27°10'S). Tropical eastern and northern Australia.

***Trimma necopina*** Whitley, 1959
Uncommon. Records from Tangalooma Wrecks, QMI29167 and Amity Pt, QMI29749 and QMI31348. A sight record from Southport seaway. Tropical to subtropical eastern Australia.

***Valenciennea immaculata*** (Ni, 1981)
Common. Kuiter (1993) stated that the Australian form of this species is a closely related but undescribed relative of the true *V. immaculata* from Chinese seas. Voucher QMI29231. Subtropical to tropical west Pacific and western Australia.

AMBLYOPINAE

***Brachyamblyopus rubristriata*** (Saville-Kent, 1889)
Common, usually found in estuarine mudbanks. Voucher QMI17467. Tropical Australia.

***Taenioides purpurascens*** (De Vis, 1884)
Common. Tropical Australia

***Trypauchen microcephalus*** (Bleeker, 1860)
Common. Tropical east Indo-west Pacific.

OXUDERCINAE

***Periophthalmus argentilineatus*** Valenciennes, 1837
Rare or now absent. Only records QMI2738 collected in 1895 and a specimen from the Brisbane R. mouth reported (as *P. koelreuteri*?, Pallas) by Castelnau (1878). Southern record. Tropical Indo-west Pacific.

***Scartelaos histophorus*** (Valenciennes, 1837)
Uncommon. Found on mudflats at Lota and mudbanks in the Brisbane R. (Townsend & Tibbits, 1995). Southern record QMI31099 from Talburpin Pt (27°39'S). Tropical north and east Indo-west Pacific.

ELEOTRIDIDAE

***Butis butis*** (Hamilton-Buchanan, 1822)
Common. Found in estuaries, penetrating into freshwater. Tropical Indo-west Pacific.

***Butis koilomatodon***
Rare. *Prionobutis wardi* Whitley, 1939 is a junior synonym (H. Larson pers. comm., 1998). Specimens dredged from Cabbage Tree Ck, QMI31027 and Nundah Ck, QMI31093 (Fig. 2L). Southern record. Tropical Indo-west Pacific.

***Eleotris melanosoma*** Bleeker, 1852
Rare. One specimen from Myora Ck mouth only. Southern record QMI31370.

***Prionobutis microps*** (Weber, 1908)
Common. Often taken by beam trawl in local estuaries. Southern record QMI28604 from Logan R. Tropical east Indo-west Pacific.

MICRODESMIDAE

***Ptereleotris heteroptera*** (Bleeker, 1855)
Rare. Only record AMSI17125-001. Tropical central and Indo-west Pacific.

***Ptereleotris microlepis*** (Bleeker, 1856)
Uncommon inside Moreton Bay. Voucher QMI29234 from Tangalooma Wrecks. Tropical central and Indo-west Pacific.

ACANTHURIDAE

***Acanthurus dussumieri*** Valenciennes, 1835
Common. Tropical central and Indo-west Pacific.

***Acanthurus grammoptilus*** Richardson, 1843
Common. Tropical Indo-Australian Archipelago.

***Acanthurus mata*** Cuvier, 1829
Rare inside Moreton Bay. Sight record by B. Hutchins from Southport seaway only. Tropical central and Indo-west Pacific.

***Acanthurus nigrofuscus*** (Forsskål, 1775)
Common. Tropical central and Indo-west Pacific.

***Acanthurus triostegus*** (Linnaeus, 1758)
Locally common at Bulwer and Southport seaway. Prefers reefs exposed to wave action. Tropical Indo-Pacific.

***Acanthurus xanthopterus*** Valenciennes, 1835
Abundant. Tropical Indo-Pacific.

***Ctenochaetus striatus*** (Quoy & Gaimard, 1825)
Rare inside Moreton Bay. Specimen, QMI31169 and a sight record, both from Southport seaway. Southern record. Tropical Indo-west Pacific.

***Naso annulatus*** (Quoy & Gaimard, 1825)
Common. Tropical central and Indo-west Pacific.

***Naso unicornis*** (Forsskål, 1775)
Common. Tropical central and Indo-west Pacific.

***Prionurus maculatus*** Ogilby, 1887
Abundant. Subtropical eastern Australia and Southwest Pacific.

***Prionurus microlepidotus*** Lacepede, 1804
Common. Subtropical eastern Australia.

***Zanclus cornutus*** (Linnaeus, 1758)
Uncommon inside Moreton Bay. Sightings from Amity Pt and Curtin Artificial Reef only. Tropical Indo-Pacific.

***Zebrasoma veliferum*** (Bloch, 1797)
Uncommon inside Moreton Bay. Tropical central and Indo-west Pacific.

SIGANIDAE

***Siganus fuscescens*** (Houttuyn, 1782)
Abundant. Kuiter (1996: 374-377) recognises *S. margaritiferus* (Valenciennes, 1835) and *S. nebulosus* (Quoy & Gaimard, 1824) from Australian waters, however Woodland (1990) regards these species as junior synonyms of *S. fuscescens*. Woodland states that the lateral spots on this species increase in number and decrease in size with age. Mature specimens of identical length have been noted locally to possess two distinct, roughly defineable size classes of spots. Adams & Woodland (1994) record the closely related *S. canaliculatus* from off nearby Maryborough (25°32'S). It may be one of the two

forms recognised above. Tropical to warm temperate east Indo-west Pacific.

***Siganus lineatus*** (Valenciennes, 1835)
Rare. Two records, QMI3169 and QMI6692. Tropical Indo-west Pacific to India.

***Siganus spinus*** (Linnaeus, 1758)
Locally common at Amity Pt and Southport seaway based on sight records only. Tropical Indo-west Pacific to India.

TRICHIURIDAE

***Trichiurus lepturus*** Linnaeus, 1758
Common. Circumglobal.

SCOMBRIDAE

***Acanthocybium solandri*** (Cuvier, 1831)
Uncommon inside Moreton Bay. Circumtropical.

***Cybiosarda elegans*** (Whitley, 1935)
Abundant. Tropical to warm temperate Australia.

***Gasterochisma melampus*** Richardson, 1845
Doubtful record. Reported by Ogilby (1912) on the basis of six specimens from the Brisbane fish market reportedly taken in Moreton Bay. Voucher QMI71. Usually an oceanic species. Southern temperate circumglobal.

***Grammatorcynus bicarinatus*** (Quoy & Gaimard, 1824)
Uncommon inside Moreton Bay, but often sighted near Flinders Reef (26°58'S). Reported by Ogilby (1918b) and Marshall (1964). No voucher specimens in QM. Subtropical eastern and western Australia.

***Rastrelliger kanagurta*** (Cuvier, 1817)
Rare. Southern record QMI26378. Tropical Indo-west Pacific.

***Sarda australis*** (Macleay, 1881)
Common. Reported by Grant (1993: 643) with a photograph of a specimen from Moreton Bay. Southeastern Australia and warm temperate southwest Pacific.

***Scomber australasicus*** Cuvier, 1831
Common. Temperate to tropical Pacific and Indo-Australian Archipelago.

***Scomberomorus commerson*** (Lacepède, 1800)
Common. Tropical to temperate Indo-west Pacific.

***Scomberomorus munroi*** Collette & Russo, 1980
Abundant. Tropical to subtropical Australia and southern New Guinea.

***Scomberomorus queenslandicus*** Munro, 1943
Abundant. Tropical Australia and southern New Guinea.

***Scomberomorus semifasciatus*** (Macleay, 1884)
Common. Tropical Australia and southern New Guinea.

***Thunnus maccoyii*** (Castelnau, 1872)
Rare. Reported by Ogilby (1908a) as *T. thynnus* (Linnaeus, 1758). Kailola et al. (1993) records northern limit as 30°00'S (near Coffs Harbour). Other scombrids, including *T. albacares* (Bonnaterre, 1788), *Euthynnus affinis* (Cantor, 1849), *Katsuwonus pelamis* (Linnaeus, 1758) and *Auxis thazard* (Lacepède, 1800) are commonly taken off Cape Moreton and have been reported by local gamefishing clubs and fishermen from within Moreton Bay, but no records have yet been verified. Southern temperate circumglobal.

***Thunnus tonggol*** (Bleeker, 1851)
Abundant. Tropical to warm temperate west Pacific, Indo-Australian Archipelago and northern Indian Ocean.

ISTIOPHORIDAE

***Istiophorus platypterus*** (Shaw & Nodder, 1791)
Common. Tropical to temperate circumglobal.

***Makaira indica*** (Cuvier, 1832)
Uncommon inside Moreton Bay. Tropical to temperate Indo-Pacific and east Atlantic.

CENTROLOPHIDAE

***Schedophilus maculatus*** Günther, 1860
Rare. Reported from Moreton Bay (as *Leirus maculatus*) by Ogilby (1916b). McDowell (1982) states that it is probably an oceanic-pelagic species found in and over deep water. As is characteristic of small stromateoids, juveniles are known from near surface waters under jellyfish. In the region, recorded from Lord Howe I., central and southern NSW and New Zealand. Northern record QMI30989. Southern temperate circumglobal.

TABLE 1. Fifteen most speciose families in Moreton Bay

| Family | Genera | Species | % of Total |
|---|---|---|---|
| Gobiidae | 35 | 44 | 5.9 |
| Labridae | 21 | 44 | 5.9 |
| Carangidae | 19 | 37 | 4.9 |
| Pomacentridae | 12 | 34 | 4.5 |
| Chaetodontidae | 7 | 28 | 3.7 |
| Serranidae | 8 | 21 | 2.8 |
| Scorpaenidae | 15 | 20 | 2.7 |
| Tetraodontidae | 6 | 20 | 2.7 |
| Apogonidae | 5 | 19 | 2.5 |
| Monacanthidae | 15 | 16 | 2.1 |
| Blennidae | 8 | 15 | 2.0 |
| Syngnathidae | 12 | 15 | 2.0 |
| Platycephalidae | 7 | 15 | 2.0 |
| Lutjanidae | 4 | 14 | 1.9 |
| Acanthuridae | 6 | 13 | 1.7 |
| Total | 180 | 355 | 47.4 |

## NOMEIDAE

***Cubiceps squamiceps*** (Lloyd, 1909)
Uncommon inside Moreton Bay. *Psenes whiteleggii* Waite, 1894 and *Psenes hilli* Ogilby, 1915 are the juveniles of this species (Butler, 1979; P. Last pers. comm., 1995). Juveniles only, all recorded from Cowan Cowan. Adults frequently trawled in over 100m depth outside Moreton Bay.

***Nomeus gronovii*** (Gmelin, 1788)
Uncommon. All records from Cowan Cowan. Tropical to warm temperate circumglobal.

## BOTHIDAE

***Arnoglossus fisoni*** Ogilby, 1898
Common. Subtropical eastern Australia.

***Arnoglossus waitei*** Norman, 1926
Uncommon. Reported as numerous in trawl samples by Weng (1988), but possibly confused with *A. fisoni*. Northern Australia.

***Engyprosopon grandisquamma*** (Schlegel, 1846)
Common. Tropical Indo-west Pacific.

***Grammatobothus pennatus*** (Ogilby, 1913)
Rare. Only record, holotype, QMI1557. Southern limit extended from Moreton Bay to to Clarence R., NSW (29°26'S) by Graham & Wood (1997). Tropical Australia.

***Lophonectes gallus*** Günther, 1880
Rare inside Moreton Bay. Reported by Ogilby (1912). Northern record QMI517. Southeastern Australia and warm temperate southwest Pacific.

***Pseudorhombus arsius*** (Hamilton, 1822)
Common. Tropical to warm temperate Indo-west Pacific.

***Pseudorhombus elevatus*** Ogilby, 1912
Rare. Only record holotype, QMI1569. Southern record. Tropical Indian Ocean and Indo-Australian Archipelago.

***Pseudorhombus jenynsii*** (Bleeker, 1855)
Abundant. Temperate to subtropical Australia.

## SOLEIDAE

***Aseraggodes macleayanus*** (Ramsay, 1881)
Common. Tropical to subtropical northeastern Australia.

***Aseraggodes*** sp.
Rare. Only record QMI29807. Colour light brown, profusely freckled with dusky spots about half size of eye; several larger spots along lateral line. Figured in Kuiter (1993: 391; 1996: 384). Subtropical eastern Australia.

***Dexillichthys*** sp.
Rare. Possibly an undescribed species. Eyes are contiguous and pectoral fin reduced. Squamation differs from *D. muelleri* (Steindachner, 1879). Known only by QMI11440 and QMI26926 from Moreton Bay. Southern record. Subtropical eastern Australia.

***Pardachirus hedleyi*** Ogilby, 1916
Common. Warm temperate to subtropical eastern Australia.

***Phyllichthys sclerolepis*** (Macleay, 1878)
Uncommon. Southern record QMI12355 from Myora. Northern to subtropical eastern Australia.

***Synaptura nigra*** Macleay, 1880
Common. Temperate to subtropical eastern Australia.

***Zebrias scalaris*** Gomon, 1987
Rare. Reported north to Moreton Bay by Gomon (1987) and Gomon et al. (1994) based on a specimen from off Moreton I., (NMVA2787). Occasionally trawled in moderate depths (35-80m) outside Moreton Bay. Record of *Z. quagga* (Kaup, 1858) from Brisbane by Castelnau (1879) almost certainly represents a misidentification of this species. Occurs north to off Pt Cartwright (26°40'S, QMI9976). Temperate to subtropical eastern Australia.

## CYNOGLOSSIDAE

***Cynoglossus bilineatus*** (Lacepède, 1802)
Uncommon. Recorded by Stephenson and Burgess (1980) and included in several unpublished reports on trawl bycatch surveys. Widespread in northern Australia. No specimens in QM. Southern limit. Tropical to subtropical northwest Pacific, Indo-Australian Archipelago and east Indian Ocean.

***Cynoglossus macculloch*** Norman, 1926
Uncommon. Frequently confused with *C. maculipinnis*, Voucher QMI30210. Tropical eastern Australia.

***Cynoglossus maculipinnis*** Rendahl, 1921
Abundant. Tropical Australia.

***Cynoglossus*** sp.
Common. Body and fins brown, without spots or mottling; individual scales with darker margins. Currently under study by T. Munroe (USNM). Voucher QMI29517-9. Subtropical eastern Australia.

***Paraplagusia bilineata*** (Bloch, 1787)
Common. Menon (1979) and Chapleau and Renaud (1993) regard *P. guttata* (Macleay, 1878) and *P. unicolor* (Macleay, 1881) as junior synonyms. Marshall (1964: 467) provided a key to separate these species in Qld waters. It appears that this key may refer to *P. bilineata* and one of the two species below. Vouchers QMI14565, QMI30652, QMI30657. Tropical Indo-west Pacific.

***Paraplagusia sinerama*** Chapleau & Renaud, 1993
Common. The appropriate name for this species is uncertain because of an apparently insoluble problem with two putative holotypes of a De Vis (1883) species, *Plagusia (=Paraplagusia) notata*, from Moreton Bay (Johnson, 1999). *Paraplagusia sinerama* was previously recorded only from north-western Australia. Southern record QMI30163, Tropical Australia.

***Paraplagusia*** *sp.*
Common. This species appears closely related to *P. bilineata*. Menon (1979) identified specimens of *P. blochi* (Bleeker, 1851) from Moreton Bay in the British Museum collection. However, Chapleau & Renaud (1993) reassessed several of the key characters employed by Menon in distinguishing these species and considered them not to be useful in defining species. They also failed to include *P. blochi* in their discussion of *Paraplagusia* known from northern Australia. The species treated here has vague pale rounded to oval spots on the ocular side whereas *P. blochi* is uniformly light brown. *Paraplagusia bilineata* differs from this species in colouration (smaller irregular pale angular spots or flecks on the ocular side) and in degree of branching to lower labial papillae (relatively sparse, often simple tuberculate branches vs numerous fimbriate or arborescent branches). In addition, although *P. bilineata* is reported to have either 2 or 3 lateral lines on the ocular side (Chapleau & Renaud, 1993), all QM specimens of *P. bilineata* have three lateral lines and specimens of the species treated here have only two. Vouchers QMI13077, QMI30691. Warm temperate to subtropical eastern Australia.

## TRIACANTHIDAE

***Triacanthus biaculeatus*** (Bloch, 1786)
Uncommon. One specimen record (AMSI-19582-001) and several reports from trawl surveys including Stephenson & Burgess (1980). Tropical west Pacific, Indo-Australian Archipelago and northern Indian Ocean.

***Tripodichthys angustifrons*** (Hollard, 1854)
Common. Tropical Indo-Australian Archipelago.

## BALISTIDAE

***Abalistes stellatus*** (Lacepède, 1798)
Uncommon inside Moreton Bay. Tropical Indo-west Pacific.

***Balistapus undulatus*** (Park, 1797)
Rare. Only record QMI303. Southern record. Tropical central and Indo-west Pacific.

***Canthidermis maculatus*** (Bloch, 1786)
Rare. Only record QMI3222, from Brisbane R. Southern record. Circumtropical.

***Sufflamen chrysopterus*** (Bloch & Schneider, 1801)
Locally common at Curtin Artificial Reef and Comboyuro Pt. Tropical to subtropical Indo-west Pacific.

***Sufflamen fraenatus*** (Latreille, 1804)
Locally common at Curtin Artificial Reef and Comboyuro Pt. Tropical to subtropical central and Indo-west Pacific.

MONACANTHIDAE

***Acreichthys tomentosus*** (Linnaeus, 1758)
Doubtful record. Only Australian specimen, QMI9237 (Hutchins pers. comm., 1997) was labelled 'Moreton Bay' but was registered from an old collection which also included specimens from the Solomon Islands. Tropical west Pacific and Indo-Malay Archipelago.

***Anacanthus barbatus*** Gray, 1831
Common. East Indian Ocean and Indo-Australian Archipelago.

***Brachaluteres jacksonianus*** (Quoy & Gaimard, 1824)
Uncommon. Temperate Australia.

***Cantherhines pardalis*** (Rüppell, 1837)
Uncommon. Voucher QMI31002. Tropical Indo-west Pacific.

***Cantheschenia grandisquamis*** Hutchins, 1977
Common. Subtropical eastern Australia.

***Chaetoderma penicilligera*** (Cuvier, 1817)
Common. Tropical west Pacific and Indo-Australian Archipelago.

***Eubalichthys mosaicus*** (Ramsay & Ogilby, 1886)
Rare. Only record QMI26225. Temperate Australia.

***Meuschenia trachylepis*** (Günther, 1870)
Abundant. Temperate to subtropical eastern Australia.

***Monacanthus chinensis*** (Osbeck, 1765)
Abundant. Tropical to warm temperate west Pacific and Indo-Australian Archipelago.

***Nelusetta ayraudi*** (Quoy & Gaimard, 1824)
Rare inside Moreton Bay. Voucher QMI308. Occurs north to off Caloundra (26°48'S), QMI30216. Temperate Australia and southwest Pacific.

***Paraluteres prionurus*** (Bleeker, 1851)
Common. Tropical eastern Australia and Indo-west Pacific.

***Paramonacanthus filicauda*** (Günther, 1880)
Uncommon inside Moreton Bay. Usually placed in *Paramonacanthus* but shown to belong to an undescribed genus by Hutchins (1997). Tropical to subtropical Australia.

***Paramonacanthus otisensis*** Whitley, 1931
Abundant. Frequently misidentified as *P. oblongus* (Schlegel, 1850). Ranked first in order of abundance of trawled fishes in Moreton Bay by Stephenson and Burgess (1980). Tropical to warm temperate eastern Australia.

***Pervagor janthinosoma*** (Bleeker, 1854)
Common. Tropical Indo-west Pacific.

***Pseudalutarius nasicornis*** (Temminck & Schlegel, 1850)
Uncommon. Tropical to subtropical Indo-west Pacific.

***Pseudomonacanthus peroni*** (Hollard, 1854)
Common. Tropical to subtropical eastern Australia.

OSTRACIIDAE

***Lactoria cornuta*** (Linnaeus, 1758)
Common. Tropical central and Indo-west Pacific.

***Lactoria diaphana*** (Bloch & Schneider, 1801)
Uncommon inside Moreton Bay. Tropical to warm temperate Indo-west Pacific.

***Lactoria fornasini*** (Bianconi, 1846)
Uncommon inside Moreton Bay. Tropical Indo-west Pacific.

***Ostracion cubicus*** Linnaeus, 1758
Common. Tropical to warm temperate Indo-west Pacific.

***Ostracion meleagris*** Shaw, 1796
Rare inside Moreton Bay. Sight record from Southport seaway only. Tropical Indo-Pacific.

***Tetrosomus concatenatus*** (Bloch, 1786)
Common. Tropical to warm temperate Indo-west Pacific.

***Tetrosomus gibbosus*** (Linnaeus, 1758)
Uncommon. Only record QMI12382. Tropical Indo-west Pacific.

TETRAODONTIDAE

***Arothron hispidus*** (Linnaeus, 1758)
Common. Tropical Indo-Pacific.

***Arothron manilensis*** (de Proce, 1822)
Common. Tropical west Pacific and Indo-Australian Archipelago.

***Arothron nigropunctatus*** (Bloch & Schneider, 1801)
Rare inside Moreton Bay. Only records QMI351 and QMI30404 from Amity Pt. Tropical Indo-west Pacific.

***Arothron stellatus*** (Bloch & Schneider, 1801)
Common. Tropical central and Indo-west Pacific.

***Canthigaster bennetti*** (Bleeker, 1854)
Common. Tropical Indo-west Pacific.

***Canthigaster callisterna*** (Ogilby, 1889)
Uncommon. Reported from Lord Howe and Norfolk I. and NSW coast by Allen & Randall (1977). Specimen from Southport, QMI1586 and a sight record from Amity Pt. Occurs north to at least Flinders Reef (26°58'S) based on personal observations (1997). Warm temperate eastern Australia and southwest Pacific.

***Canthigaster janthinoptera*** (Bleeker, 1855)
Rare. One specimen, QMI30260 from Amity Pt. Tropical Indo-west Pacific.

***Canthigaster valentini*** (Bleeker, 1853)
Common. Tropical Indo-west Pacific.

***Lagocephalus inermis*** (Temminck & Schegel, 1850)
Common. Tropical Indo-west Pacific.

***Lagocephalus lunaris*** (Bloch & Schneider, 1801)
Common. Tropical Indo-west Pacific.

***Lagocephalus scleratus*** (Gmelin, 1788)
Common. Tropical Indo-west Pacific.

***Marilyna pleurosticta*** (Günther, 1871)
Abundant. Tropical to subtropical eastern Australia.

***Tetractenos glaber*** (Freminville, 1813)
Rare. One specimen only. Northern record QMI344. Temperate eastern Australia and eastern South Australia.

***Tetractenos hamiltoni*** (Gray & Richardson, 1843)
Abundant. Warm temperate to subtropical eastern Australia and southwest Pacific.

***Torquigener altipinnis*** (Ogilby, 1891)
Uncommon inside Moreton Bay. Warm temperate to subtropical eastern Australia and southwest Pacific.

***Torquigener perlevis*** (Ogilby, 1908)
Common. Warm temperate eastern Australia to the Gulf of Carpentaria.

***Torquigener pleurogramma*** (Regan, 1903)
Abundant. Temperate to subtropical Australia.

***Torquigener squamicauda*** (Ogilby, 1911)
Abundant. Warm temperate to subtropical eastern Australia.

***Torquigener tuberculiferus*** (Ogilby, 1912)
Rare. One syntype, QMI1531 only. Southern limit extended from Moreton Bay to Clarence R., NSW (29°26'S) by Graham & Wood (1997). Tropical to subtropical eastern Australia.

***Torquigener whitleyi*** (Paradice, 1927)
Common. Southern record QMI10044. Tropical Australia.

DIODONTIDAE

***Chilomycterus reticulatus*** (Linnaeus, 1758)
Rare. Sight record from Bulwer only. Circumtropical.

***Dicotylichthys punctulatus*** Kaup, 1855
Common. Temperate to subtropical eastern Australia.

***Diodon holocanthus*** Linnaeus, 1758
Common. Tropical to warm temperate circumglobal.

***Tragulichthys jaculiferus*** (Cuvier, 1818)
Common. Tropical to subtropical Australia.

## DISCUSSION

A total of 750 species from 148 families are recorded from Moreton Bay, although references to the occurrence of 11 species are considered doubtful and cannot be verified on the basis of extant specimens or recent observations. Doubtful species have probably been reported by authors due to misidentifications or the use of a broader definition of Moreton Bay, to include nearby offshore areas. A large number of species (47.3%) are uncommon or rare. Some are vagrants that are unlikely to form breeding populations in the area. No species are endemic to the area. Several, including the unidentified species of *Ophichthus* and *Cocotropus* and the blind shark *Brachaelurus colcloughi* are poorly known within and outside the region. Two species are new records for Australia. *Carangoides dinema*, although widespread in the Indo-west Pacific, had not been recorded from Australian waters (Gunn, 1990). *Matsubaraea fusiforme* was previously known only from the northern hemisphere, from southern Japan, the Gulf of Thailand and northern waters of the Phillippines. Given the long period over which records from this area have been accumulated and its proximity to a large centre of population, the chances of obtaining outliers and rare species has been enhanced. Only 26 species reach the northern limit to their range (along the east coast of Australia) in Moreton Bay, and all but 8 of these are rare in the area and probably only occur as transients. Preliminary analysis of QM records suggest that the inclusion of adjacent offshore waters and the waters north to the vicinity of Fraser Island would create a more readily defineable ecotone which would constitute the northern range limit to significantly more subtropical or temperate species. Conversely, Moreton Bay is the southernmost large subtropical embayment on the east coast of Australia and forms the southern range limit to 132 species (17.6% of the fish fauna of Moreton Bay). Many other tropical species are found only rarely or as juveniles in waters further south. The fish fauna of Moreton Bay may be broadly categorised as comprising 385 (51.5%) reef/rocky shore, 189 (25%) demersal soft bottom, 75 (10%) estuarine and 101 (13.5%) pelagic species. Twelve species usually found at depths in excess of 40m, 15 oceanic transients and 6 freshwater species commonly found in lower estuarine areas are recorded. Many prefer habitat types that are poorly represented in the area, such as surf zones or coral reefs, or clearer oceanic waters.

The 15 most speciose families account for 47.4 percent of the fauna and the top 12 account for 41.8 percent (Table 1). Proportionally, this is broadly consistent with the estimates of Paxton et al. (1989), who found the 12 most speciose fish families in Australian waters (including freshwater species) contribute 36.8% of the Australian fish fauna. However, in the Australia-wide figures, 8 families are strongly coral reef associated, a further 2 comprise deep water inhabitants and the remaining 2 have at least half of their species in temperate regions. Moreton Bay as defined here lacks large or complex coral reef systems, is confined to depths of less than 40m and falls within a generally subtropical climatic regime. The nominal diversity of fishes listed here is large in the Australian context, although significantly enhanced by its geographic zoning between major tropical and temperate bioregions.

Comparisons with other fish faunal lists from eastern Australian tropical to warm temperate waters is complicated by habitat selectivity caused by the boundaries of the areas surveyed and their geographic location. This checklist excludes many additional species known to occur in adjacent deeper and clearer waters and around the more diverse coral reefs immediately outside Moreton Bay, such as Flinders Reef (26°58'S). Using existing QM data, preliminary estimates of the fishes of the broader Moreton Bay Marine Park (26°48'S - 27°56'S) and offshore reefs north to Fraser Island (25°00'S) are in excess of 1200 species. Surveys for a supplementary checklist covering this region are in progress.

Trinski et al. (1993) recorded 413 marine and estuarine fishes of 92 families from the Shoalwater Bay area (22°08'S - 22°40'S). This region, although proximal to the southern end of the Swain Reefs complex of the the Great Barrier Reef, has no coral reefs and most families typical of these habitats are poorly represented. Although, like Moreton Bay, there are proportionately large and diverse mangrove and seagrass communities, Shoalwater Bay is subject to much less estuarine influence and has significantly more rocky reef, with swell-exposed headlands and well developed associated algal communities. Of the Shoalwater Bay fishes, 165 (40%) are reef/rocky shore, 145 (35%) are demersal soft bottom, 65 (16%) are estuarine and 38 (9%) are pelagic species. The predominance of muddy

substrates, turbid conditions and lack of coral habitat appear to have boosted the proportions of estuarine and demersal soft bottom fishes at the expense of reef-dwelling and pelagic species, relative to the proportions prevailing in Moreton Bay. Figures (revised from Trinski et al., 1993) indicate that only 43 fish species (10.4 % of the total) have north/south range limits in Shoalwater Bay. The area forms the northern limit to 12 species and the southern limit to 31 species. In contrast, 158 or 21.1% of the fish species of Moreton Bay reach their north/south range limits in Moreton Bay.

Detailed inventories of the fishes of the Capricorn-Bunker Group (23°00'S - 24°00'S) were presented by Russell (1983) and Lowe & Russell (1990). The large and diverse system of coral reefs, interposed by relatively shallow soft bottom and some deeper shelf waters is reported to support 920 species of 121 families. There are no estuarine, mangrove or mainland inshore areas and little rocky reef within the Capricorn Bunker Group. According to Lowe & Russell (1990) coral reef species comprise 90%, demersal soft bottom 8.5% and oceanic pelagic species 1.5% of the total fauna. Checklists of the fishes of Elizabeth and Middleton Reefs (Gill & Reader, 1992) and Lord Howe I. (Francis, 1993) include 314 species of 75 families and 433 species of 88 families respectively. Both are oceanic areas encompassing mainly rocky reefal habitats with corals and littoral sandy to rocky shores. Neither include estuarine, mangrove, seagrass or inshore muddy habitats or collections from subtidal demersal soft bottom. Habitat disparities render comparitive analysis between the Moreton Bay fish fauna and that of the Capricorn-Bunker Group, Elizabeth-Middleton Reefs and Lord Howe Island difficult and emphasise the need for broader scale documentation of south-east Queensland reef fishes.

## ACKNOWLEDGEMENTS

Thanks are due to numerous colleagues for assistance in the field and for information used in the compilation of the checklist. Mark McGrouther and Sally Reader (AMS) facilitated specimen loans, access to AMS records of fishes from Moreton Bay and checked distributional data on selected species in AMS collections. Doug Hoese (AMS) and Helen Larson (NTM) provided comments on the taxonomy of Gobiid fishes. Les Knapp (USNM) assisted with platycephalids, Gerry Allen (WAM) with a pomacentrid and several apogonids and Randy Mooi (Milwaukee Public Museum) with a pempherid. Ken Graham (NSW Fisheries) gave distributional information for several scorpaenid species. John Paxton (AMS) and Peter Last (CSIRO) responded to requests for information on several groups. Martin Gomon (NMV) collaborated with a description of an undescribed stargazer. Barry Hutchins (WAM) provided personal records of observations taken at the Southport seaway. John Short, Peter Davie, John Kennedy, Steve Cook and Darryl Potter (QM) and Dennis Tafe and Maria Bavins provided valuable help on diving trips. Jeanette Covacevich (QM) provided helpful stylistic comments on the manuscript. Barry Hutchins and Martin Gomon are thanked for critically reviewing the manuscript and suggesting many helpful improvements to the final version. Finally, I thank Rolly McKay for his assistance and encouragement to undertake this study.

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ZELLER, B. 1998. Queensland's fisheries habitats – current condition and recent trends. Queensland Department of Primary Industries Information Series Q198025. Brisbane.

# NEW SPECIES AND RECORDS OF *PLAKOLANA* BRUCE (CRUSTACEA: ISOPODA: CIROLANIDAE) FROM AUSTRALIA

S.J. KEABLE

Keable, S.J. 1999 06 30: New species and records of *Plakolana* Bruce (Crustacea: Isopoda: Cirolanidae) from Australia. *Memoirs of the Queensland Museum* **43**(2): 763-775. Brisbane. ISSN 0079-8835.

Two new species of *Plakolana* are described from the continental shelf of the northern and central east coast of Australia. A revised key to the species of the genus and new records of the two other Australian species are also provided. ❐ *Isopoda, Cirolanidae, Plakolana, Australia.*

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Many species of cirolanid isopods in various genera are known to feed as scavengers on the flesh of dead or dying vertebrates (for examples see Stepien & Brusca, 1985; Bruce, 1986; Wong & Moore, 1996). These isopods may play an important role in ecosystems through the decomposition of carcasses and the associated redistribution of available energy and nutrients (Keable, 1995). They may also be significant pests of commercial fisheries (Sekiguchi, 1982; Stepien & Brusca, 1985; Berrow, 1994; Mizzan, 1995).

Cirolanid isopods in the genus *Plakolana* Bruce, 1993 are well documented scavengers which are readily collected in baited traps (Bruce, 1993; Keable, 1997) but which have rarely been collected by other means. Prior to this study 4 described species were placed in the genus. *Plakolana accola* Bruce, 1993 and *P. nagada* Bruce, 1993 are known only from trap samples collected on the outer reef slope and within the barrier reef of Madang Lagoon, northern Papua New Guinea (Bruce, 1993). These species are found in depths of 300-450m and 16-22m, respectively (Bruce, 1993). *Plakolana mandorah* Keable, 1997 has been recorded from trap samples collected in Darwin Harbour and Torres Strait, northern Australia, in depths of 8-20m (Keable, 1997). *Plakolana binyana* (Bruce, 1991) has been documented previously only from a single specimen collected in a plankton tow at a depth of 221m over a bottom depth of 355-384m, off Crescent Head, NSW, on the central east coast of Australia. Additionally, Bruce (1986) reported a single immature specimen of *Plakolana* (as *Cirolana* sp.) that does not correspond to the morphology of the described species in the genus (Bruce, 1993). This specimen was collected from off Coffs Harbour, NSW, on the central east coast of Australia in a sample of muddy sand taken from a depth of 75m.

This study documents 2 new species of *Plakolana*, and new distribution records of *P. binyana* and *P. mandorah*, apparent in collections made using baited traps in areas of NW, NE and SE Australia. To aid in the identification of these species a revised key for all species of *Plakolana* is also presented.

## METHODS

The specimens reported here were obtained mostly using the trap design outlined by Keable (1995), additional specimens of *Plakolana binyana* were also located in existing Australian Museum collections.

The terminology and procedures used in description of the new species follow those summarised by Keable (1997). Particular attention should be paid to the orientation used for the anterior and posterior margins of the pereopods which follows that indicated by Bruce (1993).

Abbreviations: AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; QM, Queensland Museum, Brisbane; WAM, Western Museum, Perth; USNM, National Museum oory, Smithsonian Institution, Washington, DC; n, number of specimens; ×, times; CE, cephalon; A1, antennule; A2, antenna; CL, clypeal region; FL, frontal lamina; MD, mandible; MP, maxilliped; MX1, maxillule; MX2, maxilla; PE, penes; PN, pleon; P1-7, pereopods 1-7; U, uropod; PL1-5, pleopods 1-5; PT, pleotelson; Qld, Queensland; NSW, New South Wales; NT, Northern Territory; Tas., Tasmania; WA, Western Australia.

## SYSTEMATICS

Class Crustacea
Order Isopoda
Family Cirolanidae

### **Plakolana** Bruce, 1993

*Plakolana* Bruce, 1993: 9; Brusca et al., 1995: 96.

TYPE SPECIES. *Plakolana accola* Bruce, 1993 by original designation.

REMARKS. A comprehensive diagnosis of *Plakolana* has been provided by Bruce (1993). In this diagnosis it is stated that the anterior margin of the basis of pereopods 4-7 is provided with long simple setae. In the generic remarks Bruce (1993) comments 'The flattened basis pereopaods [sic] 4-7 with a row of simple setae along the anterior margin, is the only character that can be recognised as a potential unique apomorphy. Nonetheless the combination of characters delimits the genus'. It should be made clear that at least on pereopod 7 (and pereopods 4-7 in material examined here) the setae forming a row on the anterior (orientation depicted by Bruce (1993) fig. 2F,H) margin of the basis are plumose, not simple (see also descriptions of *P. binyana*, *P. accola* and *P. mandorah* in Bruce (1991, 1993) and Keable (1997)). A similar arrangement of plumose setae on the basis is known in species placed in a number of other cirolanid genera such as *Aatolana* Bruce, 1993, *Bathynomus* Milne Edwards, 1879, *Dolicholana* Bruce, 1986, *Natatolana* Bruce, 1981 (see Bruce, 1986; Keable, 1996, 1997, 1998). The basis of the pereopods has also been described as flattened in both *Dolicholana* and *Natatolana* (Bruce, 1986). Therefore, on phylogenetic grounds the pereopod character described by Bruce (1993) is relatively weak in defining *Plakolana*, probably representing a plesiomorphic state or homoplasy, rather than a 'unique apomorphy'. However, as Bruce (1993) notes the size and shape of the pleonite 3 is conspicuous, with a distinct posteroventral incision and lateral rows of setae, and is unique to the species placed in *Plakolana*. Therefore, this character can be recognised as an alternative putative synapomorphy which may be used to unambiguously define the genus.

### KEY TO SPECIES OF PLAKOLANA

1. Uropod endopod, medial margin strongly sinuate distally . . . . . *P. binyana*
   Uropod endopod, medial margin straight or convex distally . . . . . 2
2. Pereopod 7, merus anterior margin without robust setae . 3
   Pereopod 7, merus anterior margin with robust setae. . 4
3. Antenna, extending to pereonite 4 or 5 when flattened along body; uropod endopod, robust seta on medial side of apex approximately equal in length to robust seta proximal to it on medial margin . . . . . *P. accola*
   Antenna, extending to pereonite 2 or 3 when flattened along body; uropod endopod, robust seta on medial side of apex approximately twice as long as robust seta proximal to it on medial margin . . . . . *P. nagada*
4. Maxilliped palp, lateral margin with plumose setae . . . . . *P. mandorah*
   Maxilliped palp, lateral margin without plumose setae . 5
5. Uropod exopod, some robust setae on medial margin longer than the exopod width lateral to their insertion; uropod endopod, lateral and medial margins forming an angle of approximately 45° at apex . . *P. acuta* sp. nov.
   Uropod exopod, all robust setae on medial margin shorter than the exopod width lateral to their insertion; uropod endopod lateral and medial margins forming an angle of approximately 60° at apex. . . . . *P. obtusa* sp. nov.

### **Plakolana acuta** sp. nov.
(Figs 1-3)

ETYMOLOGY. Derived from the latin word *acutus*, meaning sharpened, pointed or acute, refering to the appearance of the uropod endopod, as compared to some other species of *Plakolana*.

MATERIAL. HOLOTYPE: AMP54681, M, 10mm, off Flynn Reef, Qld, Australia, 16°41.32'S 146°18.26'E, baited trap, unknown substrate, 100m, J. Lowry, P. Freewater & W. Vader, 7-8 June 1993, SEAS QLD-937. PARATYPES: QMW24682, M, F; AMP47679, 5 F's; BMNH1999.462, F; USNM288442, F; all same data as holotype. OTHER MATERIAL: AMP54682, 40 specimens, east of Flynn Reef, Qld, 16°41.32'S 146°18.26'E, baited trap, unknown substrate, 100m, J. Lowry & K. Dempsey, 19-20 May, 1994, SEAS QLD-1055.

DIAGNOSIS. Dorsal interocular furrow distinct, not extending across the cephalon. Medial interocular furrow distinct, extending across the cephalon. Pleotelson robust setae present, 4-6 altogether. Antenna of medium length, 0.34× as long as body, when extended against the body reaching to posterior of pereonite 3. Maxilliped palp lateral margin plumose setae absent. Pereopod 7 merus anterior margin with robust setae. Uropod endopod robust setae long, 22% length of lateral margin; medial margin convex; lateral and medial margins forming an angle of approximately 45° at apex; robust seta on medial side of apex subequal to robust seta proximal to it on medial margin; lateral margin straight. Exopod medial margin with some robust setae longer than the exopod width lateral to their insertion.

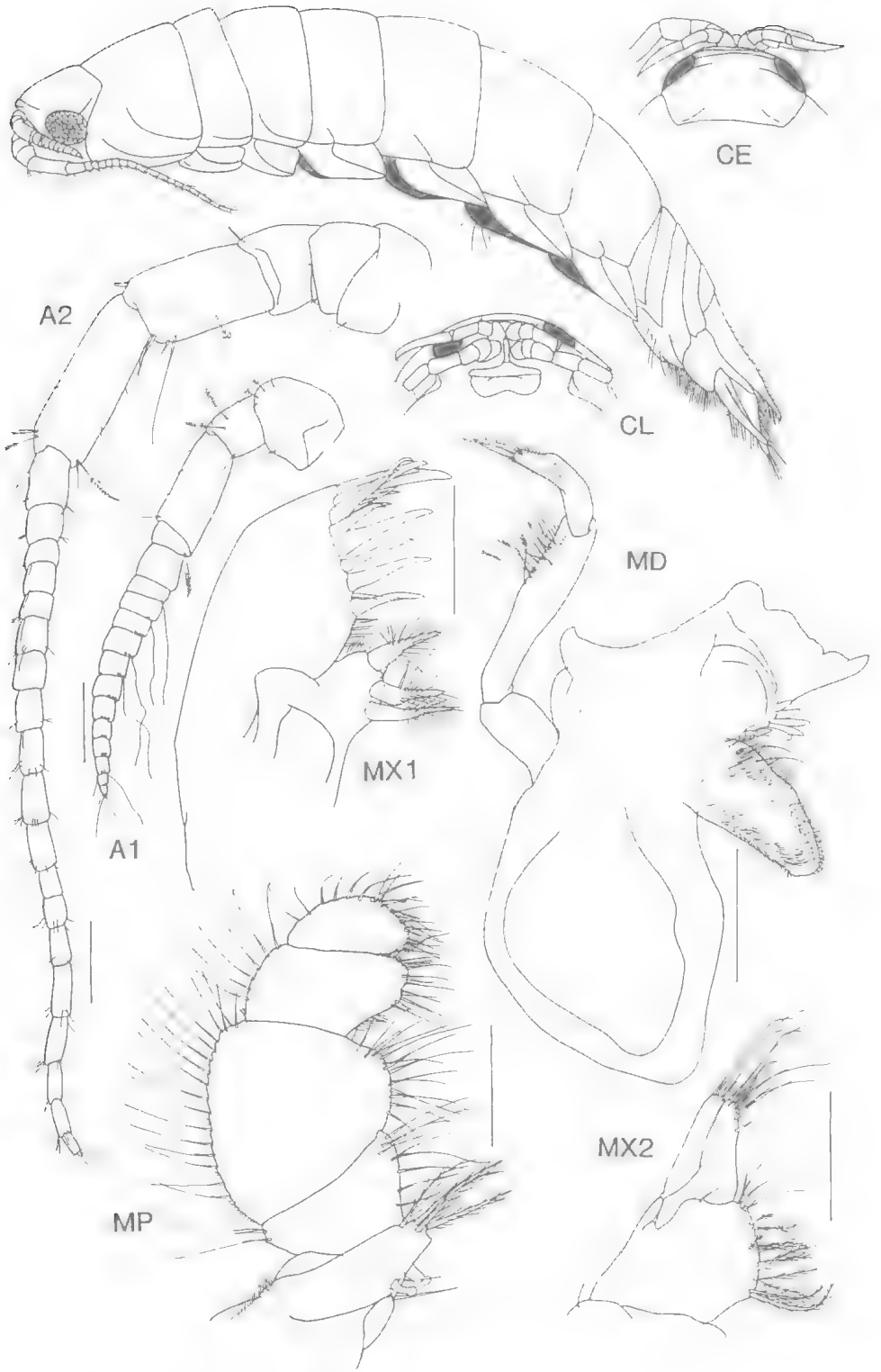



FIG. 1. *Plakolana acuta* sp. nov. Holotype. Scalebars = 0.2mm.

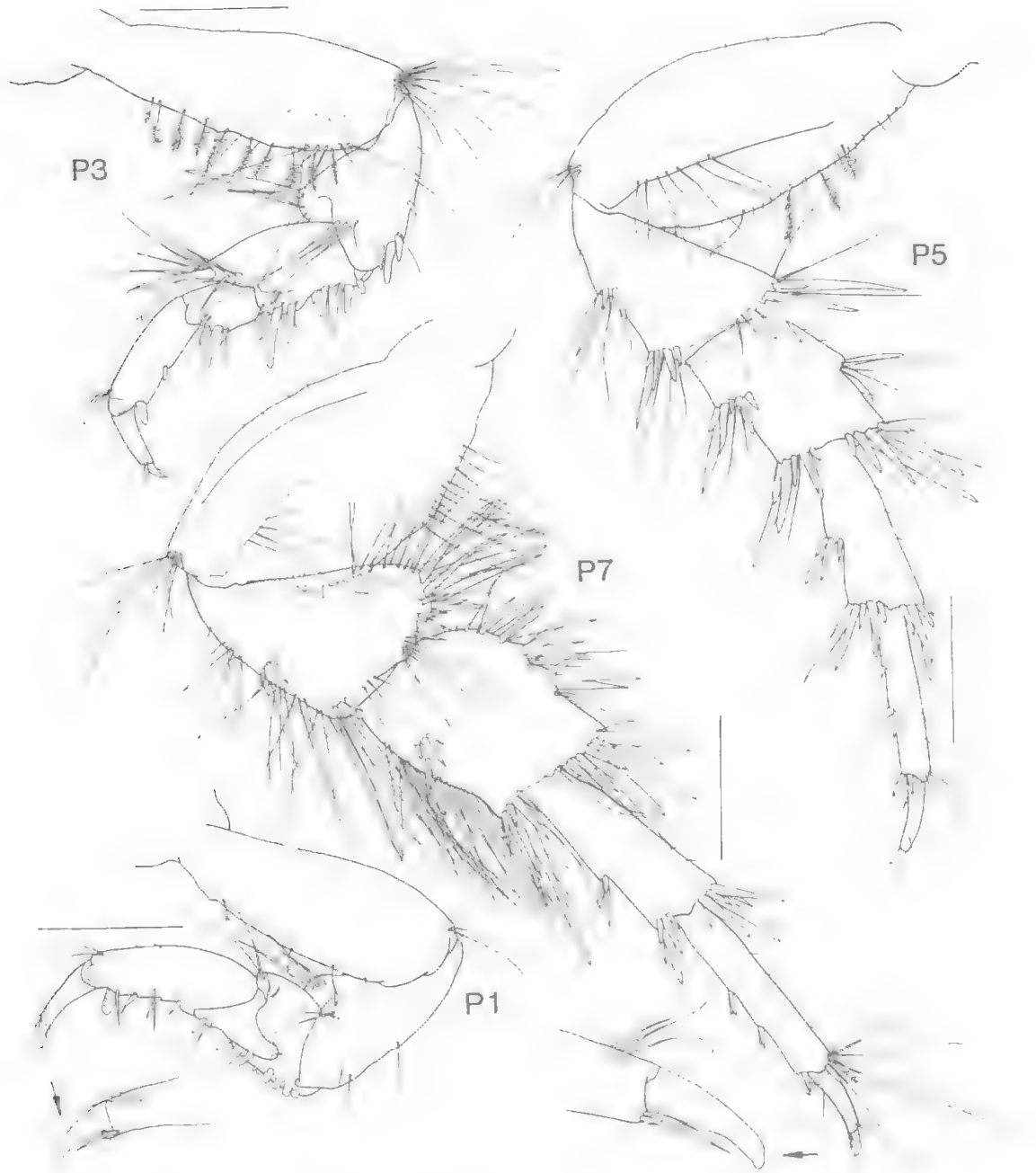



FIG. 2. *Plakolana acuta* sp. nov. Holotype. Scalebars = 0.5mm.

DESCRIPTION (Holotype).

*Overall body form.* 10mm long; narrow, length approximately 3.1× greatest width. Colour cream in alcohol. Chromatophores absent. Cuticular surfaces scale-like.

*Cephalon.* Ornamentation other than furrows or ridges absent, surface smooth; rostrum bent ventrally, anterior margin recessed in dorsal view (weakly recessed), rostrum not extending to frontal lamina, not dividing antennules; anterior

margin not overriding antennules; cephalic ridges absent, submarginal cephalic furrow well developed, runs entire length of anterior margin to eyes. Eyes present, well developed; visible in ventral view; moderate in size, round, length less than 2× height; colour cream in alcohol; partially overlapped by pereonite 1; ommatidia arranged in rows, 8 ommatidia in horizontal diameter, 7 ommatidia in vertical diameter. Dorsal interocular furrow distinct, not extending across the cephalon. Medial interocular furrow distinct, extending across the cephalon. Frontal lamina linear, length approximately 3× basal width; forming an angle of ~45° with ventral surface of cephalon; ventral surface flat, not produced; lateral margins medially constricted; lateral margins concave; ventral surface not sculpted; apex anteriorly projecting, visible in dorsal view, expanded, in 1 plane (not 'stepped'), anterior margin rounded. Clypeus triangular; width greater than length; not sculpted. Labrum flat; narrower than clypeus.

*Pereonites*. 1 longest, 2 shortest, 3-7 subequal; without transverse carina; tubercles absent.

*Pleonites*. 5 visible but pleonite 1 almost completely concealed along dorsal margin by pereonite 7; tubercles absent. Pleonite 1 posterolateral margins produced ventrally. Pleonite 2 dorsal posterolateral margin clearly projecting posterior to ventral posterolateral margin; ventral posterolateral margin acute, formed into short process. Pleonite 3 posterolateral margins extending posterior to posterodorsal margin of pleonite 5, acute with ventral incision and two rows of setae. Pleonite 4 posterolateral margins less produced than those of pleonite 3; ventral margin enclosed by pleonite 3; posterodorsal margin sinuate, convex proximal to meeting ventral margin at apex, apex broadly rounded dorsally, but meeting convex ventral margin at a point, extending posterior to posterodorsal margin of pleonite 5.

*Pleotelson*. Length 1× basal width; dorsal surface with tubercles and carinae absent; conspicuous fine setae absent from dorsal surface; anterodorsal depression absent; anterodorsal uropodal sutures on anterolateral margins present (indistinct); anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins convex; apex not produced, lateral margins meeting smoothly to a point; robust setae present, 6 altogether, 3 on each posterolateral margin; plumose setae present, restricted to posterolateral margins, moderately abundant, numerous proximal to robust setae.

*Antennule*. Short, just reaching pereonite 1. Peduncular bases touching (just); article 1 length subequal to width, greater than article 2; article 2 width subequal to length, anterodistal angle with 2 pappose setae, posterodistal angle with 1 slender seta; article 3 shorter than combined lengths of articles 1-2, longer than article 1, length greater than width. Flagellum longer than peduncle; not formed into callynophore; articles not compressed (lengths of most greater than half width); 13-articulate; article 1 short, length not much greater than width; aesthetascs present, iridescent (weakly).

*Antenna*. Medium length, 0.34× as long as body, when extended against the body reaching to posterior of pereonite 3. Peduncular article 2 shorter than article 3; article 4 slightly longer than article 3, anterodistal angle with 2 slender setae, posterolateral margin with 1 penicillate seta, posterodistal angle with 4 slender setae; article 5 longer than article 4 and all other articles, anterodistal angle with 4 slender and 1 penicillate setae, posterodistal angle with 1 slender and 1 penicillate setae. Flagellum 20-articulate; setal brush absent.

*Mandible*. Molar well developed; medial surface covered with short fine slender setae, cluster of long slender setae proximally present, long slender setae submarginal to anterior margin absent; robust setae present on anterior margin, close set. Setal row well developed, with 7 robust setae; intermediate slender setae absent; medial surface without setae. Incisor broad (wider than narrowest width of mandible), tridentate, posterior tooth larger than others. Palp article 1 longer than article 3; article 2 of medium length, approximately 2× the length of article 3, with numerous slender and serrate setae.

*Maxillule*. Medial lobe with 3 large robust pappose setae, subequal in length; lateral margin with protuberance well developed. Lateral lobe with 13 robust setae on distal surface.

*Maxilla*. Lateral lobe subequal and distinct from middle lobe; slender, with 5 slender setae. Medial lobe with 5 slender and 11 plumose setae, with 2 medial plumose setae longest and bent. Middle lobe with 10 slender setae.

*Maxilliped*. Palp moderately setose; medial margin slender setae along most of the length of articles 2-5; lateral margin slender setae along most of the length of articles 2-5, plumose setae absent; article 1 without transverse setal row; article 3 length subequal to breadth, distal margin width greater than proximal margin of article 4;

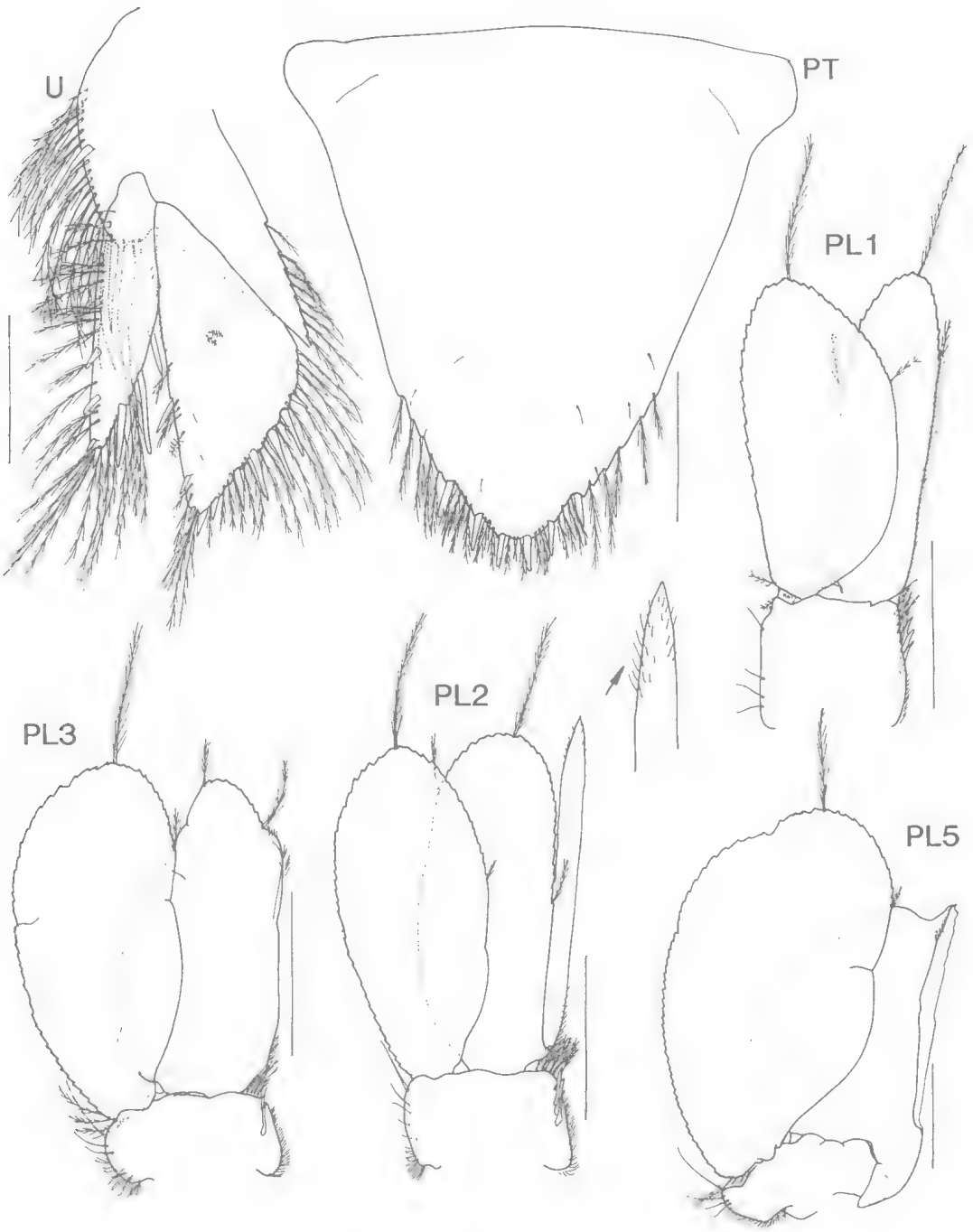



FIG. 3. *Plakolana acuta* sp. nov. Holotype. Scalebars = 0.5mm.

article 4 length less than breadth, distal margin width greater than proximal margin of article 5; article 5 rounded, length less than breadth, medial margin serrate setae present. Endite forming a distinct lobe, extending to distomedial margin of palp article 2; right endite with 2 coupling hooks, left endite with 2 coupling hooks, and 4 plumose setae.

*Coxal plates*. Shallow, not as high as long; furrows strongly developed, on all coxae.

*Pereopods*. Pereopods 1-7 dactylus secondary unguis slender and lying against primary unguis. Pereopods 1-3 merus posterior margin robust setae strongly molariform on pereopod 1 only. Pereopod 1 posterior margin setose fringe absent. Ischium anterodistal angle without robust setae; posterior margin without robust setae. Merus anterodistal angle without robust setae; posterior margin with 9 robust setae. Carpus posterior margin with 1 robust seta. Propodus robust; with 3 robust setae on palm, with 1 robust seta opposing dactylus. Dactylus long, 0.5-1× propodus length. Pereopod 2 ischium anterodistal angle with 1 robust seta; posterior margin with 2 robust setae. Merus anterodistal angle with 2 robust setae; posterior margin with 9 robust setae. Carpus with 3 robust setae. Propodus with 1 robust seta on palm, 1 robust seta opposing dactylus. Pereopod 3 ischium anterodistal angle with 1 robust seta; posterior margin with 4 robust setae. Merus anterodistal angle with 2 robust setae (and 1 set further back); posterior margin with 8 robust setae (and 1 set further back). Carpus with 3 robust setae. Propodus with 1 robust seta on palm, 1 robust seta opposing dactylus. Pereopods 4-7 basis anterior margin plumose setae present. Pereopod 7 basis of medium breadth, width 0.49× length; anterior margin setae plumose, present along entire length, closely and regularly spaced along entire length; medial carina setae slender, posterior margin setae absent; posterodistal angle setae slender. Ischium anterior margin without robust setae, non-robust setae slender; anterodistal angle with 12 robust setae (including 3 uniserrate), slender setae present; posterior margin with 2 robust setae, slender setae present; posterodistal angle with 4 robust setae, non-robust setae slender. Merus anterior margin with 6 robust setae, slender setae present; anterodistal angle with 9 robust setae, slender setae present; posterior margin with 7 robust setae, slender setae present; posterodistal angle with 8 robust setae, non-robust setae slender. Carpus anterior margin without robust setae, non-robust setae absent; anterodistal angle with 7 robust setae, non-robust setae absent; posterior margin with 3 robust setae, non-robust setae absent; posterodistal angle with 5 robust setae, non-robust setae slender (1 present). Propodus anterior margin without robust setae, non-robust setae absent; anterodistal angle with 1 robust seta, slender setae present; posterior margin with 4 robust setae, non-robust setae absent; posterodistal angle with 2 robust setae, slender setae absent.

*Penes*. Absent, vasa deferentia opening flush to surface of sternite 7.

*Pleopods*. Exopod suture incomplete on pleopods 3-5; endopod plumose setae present across distal margins of pleopods 1-4 and absent on pleopod 5. Pleopods 1-2 exopod broader than endopod; exopod and endopod elongate (length more than 2× width). Pleopod 1 exopod medial margin oblique, proximolateral robust seta absent; endopod length subequal to exopod, lateral margin concave. Pleopod 2 *appendix masculina* arising sub-basally; extending beyond tip of endopod, 1.05× length of endopod from insertion point; margins straight, approximately parallel along entire length; slender; apex not at angle to margins, acute. Pleopods 3-4 endopod distinctly shorter than exopod. Pleopod 5 peduncle lateral margin with broad, lamellar lobe; exopod distal margin rounded; endopod distal margin narrowed to obscure point, proximomedial lobe strongly produced.

*Uropods*. Extending beyond pleotelson. Peduncle ventrolateral angle with 1 robust seta, and 3 plumose setae; lateral margin robust seta present; distolateral angle rounded. Endopod medial margin convex, with 6 robust setae, robust setae long, 22% length of lateral margin, plumose setae present, along entire length, long; lateral and medial margins forming an angle of approximately 45° at apex; apex entire, without notch, with 2 robust setae, robust seta on medial side subequal to robust seta proximal to it on medial margin, setal cluster present, formed by plumose setae; lateral margin straight, with 2 robust setae, plumose setae present, on distal half (sparse), short. Exopod slightly shorter than endopod, 0.8× the length of the endopod; medial margin convex, with 3 robust setae, some robust setae longer than the exopod width lateral to their insertion, plumose setae present, not along entire length (on distal half), long; lateral and medial margins forming an angle of approximately 35° at apex; apex entire without notch and acute, with 2 robust setae, setal cluster present, formed by plumose setae; lateral margin convex, robust and plumose setae continuous along margin, with 5 robust setae, robust setae small, plumose setae present, along entire length, long.

SEXUAL DIMORPHISM. Females differ from males only in the primary sexual characters and do not have the pleopod 2 appendix masculina.

VARIATION. Pleotelson and uropod robust setal counts from margins (N = 9, all paratypes): Pleotelson 2:2 (11%), 2:3 (33%), 3:3 (56%). Endopod (medial) 5 (44%), 6 (56%); (lateral) 2 (100%). Exopod (medial) 4 (100%); (lateral) 4 (11%), 5 (89%).

SIZE RANGE. Adults 10-15mm.

REMARKS. See discussion section.

DISTRIBUTION. Australia, off Cairns, Qld. In depths of 100m.

**Plakolana obtusa** sp. nov.
(Figs 4-6)

ETYMOLOGY. Derived from the latin word *obtusus*, meaning blunt, and refers to the appearance of the uropod endopod in this species when compared to most of the other species of *Plakolana*.

MATERIAL. HOLOTYPE: AM54683, M, 9.5mm, east of Fitzroy Reef, Great Barrier Reef, Qld, Australia, 23°32.53'S 152°16.44'E, baited trap, unknown substrate, 100m, J. Lowry & K. Dempsey, 3-4 June 1994, SEAS QLD-1096. PARATYPES: QMW24683, M, F; AMP-54684, 8M's, 23F's; BMNH1999.463-464, M, F; USNM-288443, M, F, all same data as holotype. OTHER MATERIAL: AMP54685, 9 specimens, east of Flynn Reef, Qld, 16°41.32'S 146°18.26'E, baited trap, unknown substrate, 100m, J. Lowry & K. Dempsey, 19-20 May 1994, SEAS QLD-1055; AMP48439, 39 specimens, NE of Coffs Harbour, NSW, 30°15.94'S 153°21.9'E, baited trap, unknown substrate, 100m, J. Lowry & K. Dempsey, 9-10 Sept. 1994, SEAS NSW-1006.

DIAGNOSIS. Dorsal interocular furrow distinct, not extending across the cephalon. Medial interocular furrow distinct, extending across the cephalon. Pleotelson robust setae present on margins, 6 altogether. Antenna 0.35× as long as body, when extended against the body reaching to posterior of pereonite 3. Maxilliped palp lateral margin plumose setae absent. Pereopod 7 merus anterior margin with robust setae. Uropod endopod robust setae short, 11% length of lateral margin; medial margin convex; lateral and medial margins forming an angle of approximately 60° at apex; robust seta on medial side of apex shorter than robust seta proximal to it on medial margin; lateral margin slightly convex. Exopod medial margin robust setae shorter than the exopod width lateral to their insertion.

DESCRIPTION (Holotype). Due to the similarity of this species to *P. acuta* only variations between the 2 species are included here.

*Overall body form*. 9.5mm long; length approximately 2.79× greatest width.

*Cephalon*. Eye colour pale orange in alcohol; 9 ommatidia in horizontal diameter, 8 ommatidia in vertical diameter. Frontal lamina lateral margins straight, parallel.

*Pereonites*. 1 and 5-6 subequal in length and longest, 4 and 7 subequal and longer than 2-3 which are subequal.

*Pleotelson*. Length 1.05× basal width; anterolateral margins convex; robust setae present, 6 altogether.

*Antennule*. Peduncular article 1 length subequal to article 2; article 2 longer than wide. Flagellum 12-articulate; article 1 elongate, length much greater than width.

*Antenna*. 0.35× as long as body. Peduncular article 4 much longer than article 3, posterolateral margin with 1 penicillate seta, posterodistal angle with 4 slender setae, distal margin with 1 penicillate and 1 slender setae, anterodistal angle with 3 slender setae; article 5 anterodistal angle with 2 penicillate and 2 slender setae, posterodistal angle with 2 penicillate and 2 slender setae. Flagellum 25-articulate.

*Mandible*. Setal row with 9 robust setae. Palp article 1 subequal to article 3.

*Maxillule*. Medial lobe with 3 large and 1 smaller robust pappose setae, large medial seta subequal in length to large lateral setae; lateral margin with protuberance absent.

*Maxilla*. Medial lobe with 6 slender and 8 plumose setae. Middle lobe with 11 slender setae.

*Maxilliped*. endite not reaching distomedial margin of palp article 2; left endite with 7 plumose setae.

*Pereopods*. Pereopod 1 merus posterior margin with 8 robust setae. Carpus posterior margin with 2 robust setae. Pereopod 2 ischium posterior margin with 3 robust setae. Merus posterior margin with 7 robust setae. Pereopod 3 ischium posterior margin with 3 robust setae. Merus posterior margin with 9 robust setae. Pereopod 7 basis broad, width 0.56× length. Ischium anterodistal angle with 9 robust setae; posterior margin without robust setae; posterodistal angle with 2 robust setae. Merus anterodistal angle with 8 robust setae; posterior margin with 3 robust setae; non-robust setae absent. Carpus anterior margin non-robust setae slender; posterior margin with 4 robust setae, non-robust setae slender; posterodistal angle with 7 robust setae. Propodus anterior margin with non-robust setae slender. Pleopod 2 appendix masculina arising basally;

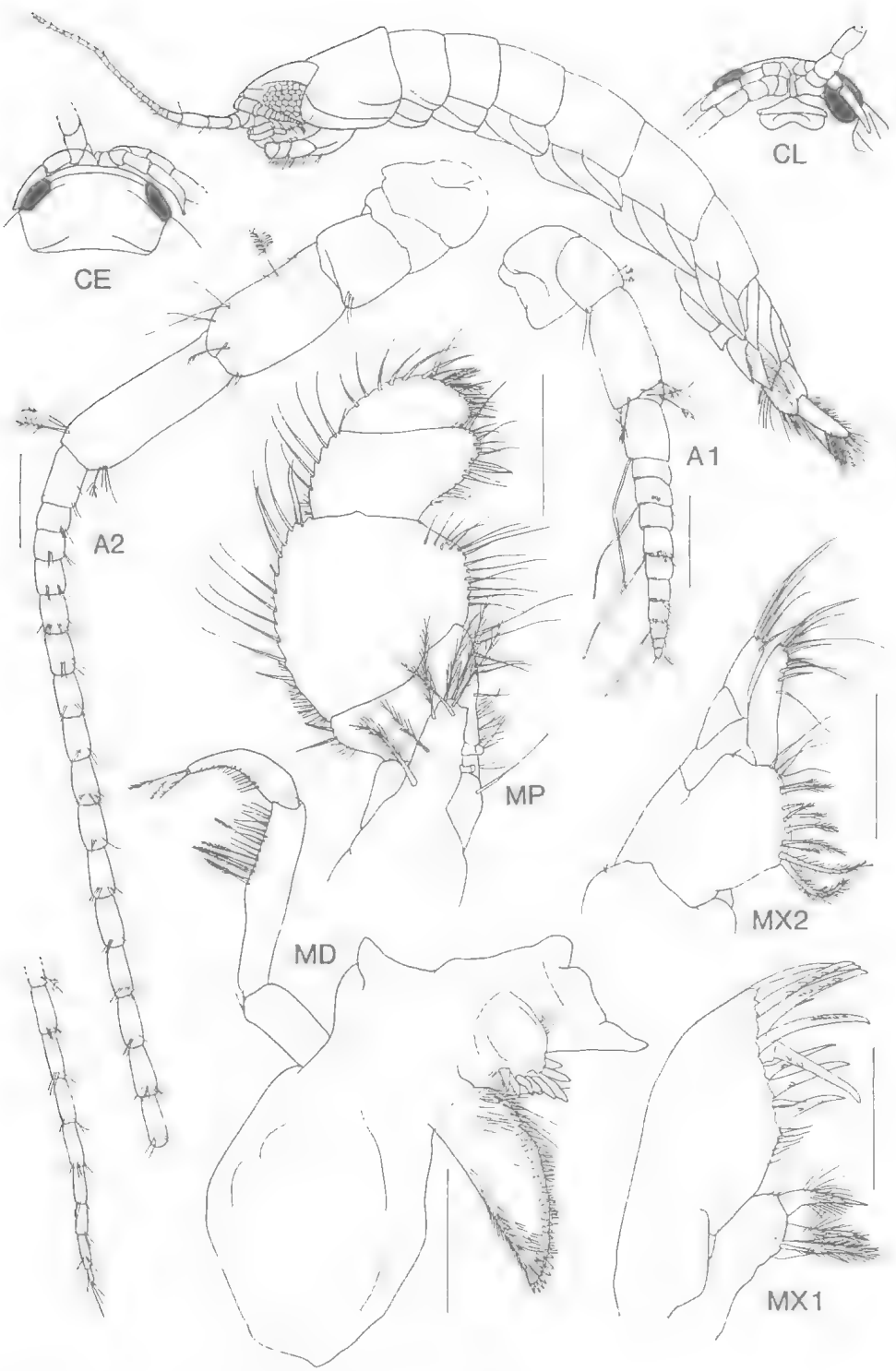



FIG. 4. *Plakolana obtusa* sp. nov. Holotype. Scalebars = 0.5mm.

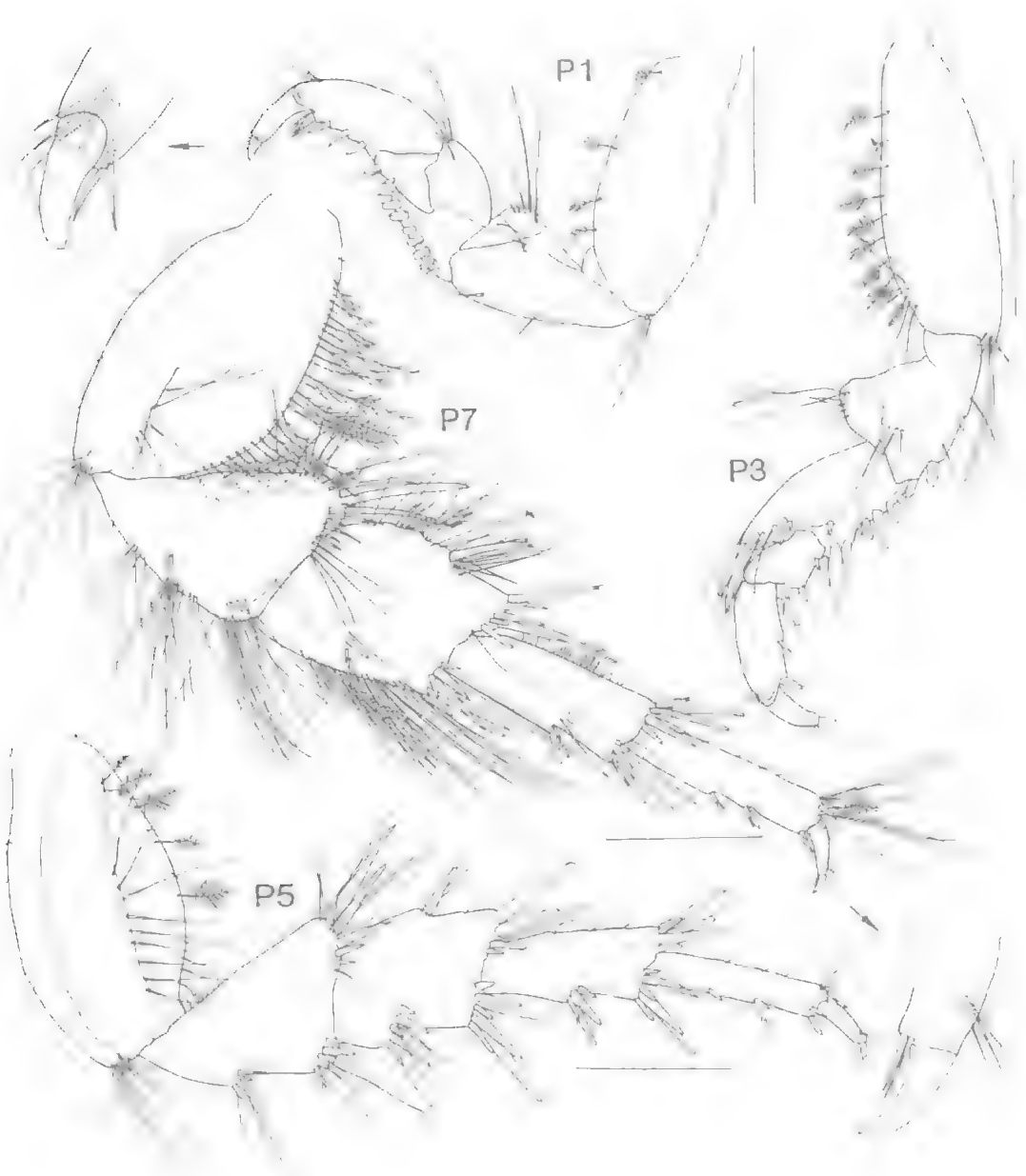



FIG. 5. *Plakolana obtusa* sp. nov. Holotype. Scalebars = 0.5mm.

extending subequal with tip of endopod, 1× length of endopod from insertion point.

*Uropods*. peduncle ventrolateral angle with 2 robust setae. Endopod robust setae short, 11% length of lateral margin; lateral and medial margins forming an angle of approximately 60° at apex; apex seta on medial side shorter than robust seta proximal to it on medial margin; lateral margin slightly convex. Exopod short, 0.79× the length of the endopod; with 4 robust setae, robust setae shorter than the exopod width lateral to their insertion; lateral and medial margins forming an angle of approximately 50° at apex; lateral margin robust setae large.

SEXUAL DIMORPHISM. Females differ from males only in the primary sexual characters and do not have the pleopod 2 appendix masculina.

VARIATION. Pleotelson and uropod robust setal counts from margins (N=20, subsample of 10 male and 10 female paratypes): Pleotelson 3:3 (100%). Endopod (medial) 5 (25%), 6 (60%), 7 (15%); (lateral) 2 (95%), 3 (5%). Exopod (medial) 4 (100%); lateral 5 (65%), 6 (35%).

SIZE RANGE. Adults 7-12mm.

REMARKS. See discussion section.

DISTRIBUTION. Australia, off Cairns and Gladstone, Qld, and Coffs Harbour, NSW. In depths of 100m.

**Plakolana binyana** (Bruce)

*Cirolana binyana* Bruce, 1991: 265, figs 4-6; Springthorpe & Lowry, 1994: 40.
*Plakolana binyana*: Bruce, 1993: 11.

MATERIAL. AMP54686, 2M's, F, east of Long Reef, NSW, 33°43-44'S 151°46'E, prawn trawl fitted with epibenthic sledges, 174m, FRV Kapala, 19 Dec. 1985, K85-21-08; AMP44239, 5M's, F, off Wollongong, NSW, 34°31.48'S 151°13.22'E, baited trap, *Globigerina* ooze, 200m, J. Lowry & K. Dempsey, 28 Mar. 1994; AM P54687, M, 400m off small shingle beach, north end of Tower Bay, D'Entrecasteaux Channel, Tas., 43°23.6'S 147°2.4'E, baited trap, unknown substrate, 40m, J. Lowry & S. Keable, 20-21 April 1991, TAS-222.

REMARKS. The material examined matches the original description of *Plakolana binyana* in all of the characters which are currently considered to be diagnostic of that species. Additional material, collected off Wollongong in depths of 200m, is also registered in Australian Museum collections (personal observation).

DISTRIBUTION. Australia, central NSW to eastern Tas. In depths of 40-221m.

**Plakolana mandorah** Keable

*Plakolana mandorah* Keable, 1997: 270, figs 8-10.

MATERIAL. AMP54688, 7F's, manca; WAMC24364, M, F; both lots from Ngalaguru (High Cliffy) I., off Kimberley Plateau, WA, 15°54.77'S 124°20.68'E, baited trap, unknown substrate, unknown depth, F. Wells, 22-23 Nov. 1994, Stn. 16.

DISTRIBUTION. Australia, Torres Strait, Qld.; Darwin, NT; off Kimberley Plateau, WA. In depths of 8-20m.

## DISCUSSION

*Plakolana acuta* and *P. obtusa* differ most noticeably from *P. accola* and *P. nagada* in having pereopod 7 with robust setae on the anterior margin of the merus. *Plakolana obtusa* also differs from these 2 species in having: the distal section of the uropod endopod medial margin noticeably convex rather than approximately straight; relatively short robust setae on the margins of the uropod endopod (approximately 11% of the length of the lateral margin of the endopod as opposed to 18% and 32-35%, respectively); the uropod endopod lateral margin convex, instead of weakly sinuate or straight; and the uropod endopod margins forming an angle of approximately 60° at the apex, instead of approximately 40° or less. *Plakolana binyana* is similar to *P. acuta* and *P. obtusa* but lacks robust setae on the anterior margin of the merus of pereopod 7, and has the medial margin of the uropod endopod sinuate, making the apex appear more distinctly narrowed. *Plakolana binyana* also has only 4 robust setae on the pleotelson whereas *P. obtusa* is only known to have 6. *Plakolana mandorah* differs most clearly from *P. acuta* and *P. obtusa* in having plumose setae on the lateral margins of the maxillipedal palp. *Plakolana mandorah* also has the margins of the uropod endopod meeting at a more acute angle (approximately 50°) than in *P. obtusa* (approximately 60°). *Plakolana acuta* and *P. obtusa* occur sympatrically and are extremely similar. *Plakolana acuta* differs from *P. obtusa* in having the margins of the uropod endopod meeting at a more acute angle (approximately 45° rather than approximately 60°) and robust setae on the medial margin of the uropod exopod which are longer than the uropod exopod width lateral to their insertion. The manca specimen Bruce (1986, 1993) recorded from Coffs Harbour, NSW, has not been assigned to a described species of *Plakolana* and differs from *P. acuta* and *P. obtusa* in having a complete dorsal interocular furrow, the anterior margin of the merus of pereopod 6 or 7 without robust setae (note that Bruce (1986) records the specimen as a manca but illustrates a pereopod 7 although this appendage is not developed in mancas) and the uropod endopod margins meet at a more obtuse angle. This suggests a further undescribed species of *Plakolana* occurs within the area where *P. obtusa* is found.

## ACKNOWLEDGEMENTS

I thank J. Lowry and P. Berents for making the material described here available for me to study, and F. Wells for collecting and donating the

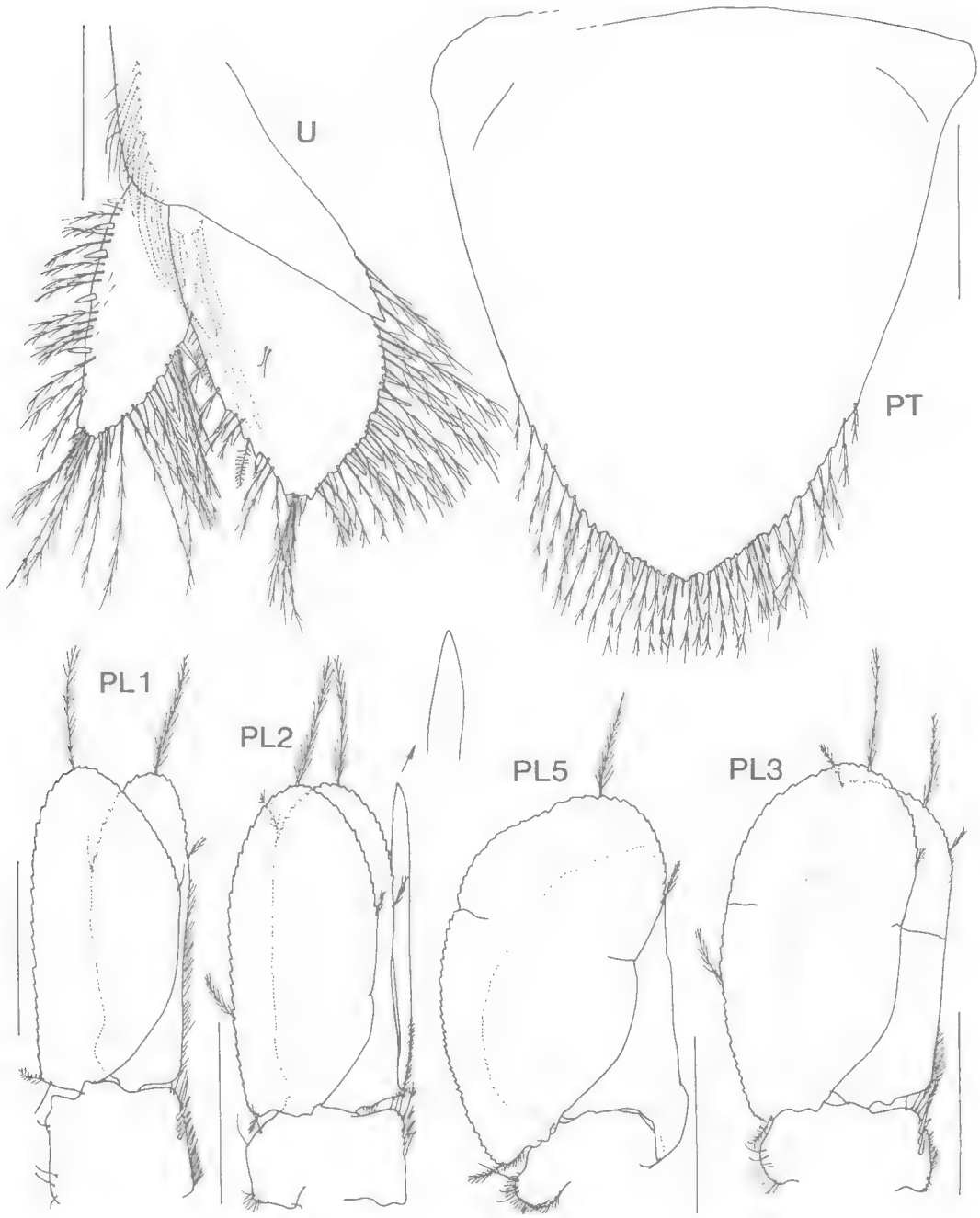



FIG. 6. *Plakolana obtusa* sp. nov. Holotype. Scalebars = 0.5mm.

material reported from Western Australia. N. Bruce and R. Brusca kindly provided unpublished character lists for cirolanid isopods which were useful in writing the species descriptions. I am also grateful to G. Wilson for comments on an initial draft of the manuscript, and to R. Springthorpe who composed and inked the plates of my illustrations. This study was undertaken while in receipt of an Australian Museum Collection Visiting Fellowship.

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**SCENT GLAND HAIR IN THE MARSUPIAL GLIDERS, *PETAURUS NORFOLCENSIS* AND *PETAURUS BREVICEPS*.** *Memoirs of the Queensland Museum 43(2): 776 1999* - Structural differentiation of hair from cutaneous glandular regions has been observed in a wide range of eutherian mammals. Referred to as osmetrichia, these specialised hairs facilitate the retention and/or dispersal of scent-gland secretions. The presence of osmetrichia in marsupials has not been established. This note reports on the examination of scent gland hairs in two species of gliding possum from the genus *Petaurus*, which rely upon cutaneous scent glands for social cohesion (Schultze-Westrum, 1969). Osmetrichia were not found in these species.

Samples were obtained from adult animals housed in captivity (University of Queensland). Hairs were collected from the frontal and sternal scent glands of four male *Petaurus breviceps* and four male *P. norfolcensis*. For comparative purposes, samples were also collected from adult females which do not possess these glands (two *P. breviceps*, three *P. norfolcensis*), and from the dorsal body surface (of both males and females). Hairs were collected from both directly above the gland surface and from the area surrounding the gland. In the case of females, hairs were collected from the region corresponding to gland location in males. Hairs were cleaned in a series of hexane and ethanol washes (as per Balakrishnan 1987) and processed for SEM (to determine surface features of the cortex) and light microscopy (to examine medullary structure).

Hairs from non-glandular body regions showed no variation from the scale patterns reported in Brunner & Coman (1974) in either species (Fig. 1A). Hairs from gland samples also showed no variation from patterns reported by Brunner & Coman (1974). Gland secretions were observed on the hair surface and clinging to scales in many samples (Fig. 1B), however, the scale patterns of these hairs did not differ from those of other body regions or from females. Some scales did radiate away from the cortex to form intercuticular spaces which held glandular secretion (Fig.1C), but similar structures were also observed in the proximal half of body hair from non-glandular regions, as illustrated in Brunner & Coman (1974: 105, fig. h; 107, fig. h).

Longitudinal grooves or ridges were observed occasionally in samples from sternal and frontal glands. These were not observed in samples from non-glandular regions or in samples collected from females and may therefore facilitate retention/storage of glandular products. The low prevalence of such hairs in samples (4%) however, indicate that this is probably a preparation artefact, and a similar effect is known to result from processing of human hair (D. MacGregor, pers. comm.). Longitudinal sectioning of hair revealed no compartmentalising of medullae in any samples.

We conclude that the scent gland hair of *P. breviceps* and *P. norfolcensis* does not exhibit sufficient structural specialisation to warrant classification as osmetrichia. Osmetrichia in eutherian mammals are a functional adaptation associated with chemical communication (e.g. Balakrishnan, 1987; Muller-Schwarze et al., 1977). They might then, also be expected to occur in Petaurid gliders. The absence of osmetrichia in this group suggests that effective pheromone transfer may be achieved simply by rubbing the gland surface (which is often bald in socially dominant males) against objects/conspecifics (see Russell, 1984). Osmetrichia have recently been described in a dasyurid marsupial *Antechinus stuartii* (Tofiegaard & Bradley, in press). The authors describe ridges and grooves on what appear to be normal cuticular scales and speculate on the importance of these structures in retaining sebum containing putative volatile pheromones. We suggest that the evidence presented by these authors requires confirmation, and that further quantitative and comparative studies of scent glands and hairs is needed to clarify their roles in the Marsupialia.

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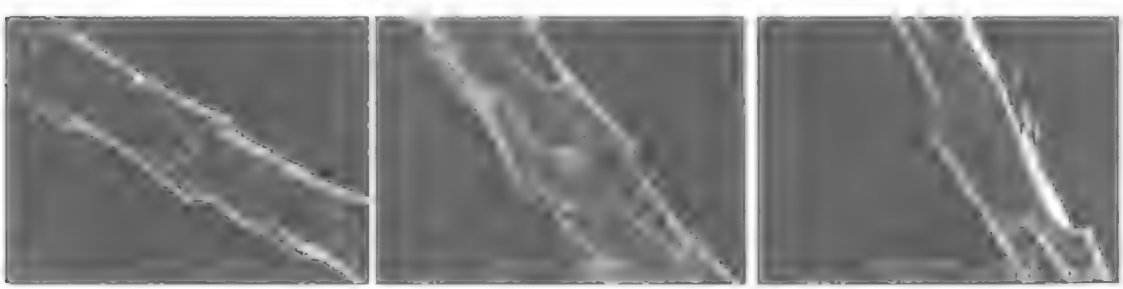


FIG. 1. A, Typical scales from the proximal half of non-glandular hair in *P. norfolcensis*, dentate margins. B, Glandular residue adhering to scales from the proximal half of hair from sternal gland of *P. norfolcensis*. C, Radiating scales forming intercuticular spaces holding glandular residue, from frontal gland of *P. breviceps*.

# RECENT COLONISATION OF HERON ISLAND, SOUTHERN GREAT BARRIER REEF, BY THE MOURNING GECKO, *LEPIDODACTYLUS LUGUBRIS*

COLIN J. LIMPUS, DUNCAN J. LIMPUS AND ALAN GOLDIZEN

Limpus, C.J., Limpus, D.J. & Goldizen, A. 1999 06 30: Recent colonisation of Heron Island, southern Great Barrier Reef, by the Mourning Gecko, *Lepidodactylus lugubris*. *Memoirs of the Queensland Museum* **43**(2): 777-781. Brisbane. ISSN 0079-8835.

The Mourning Gecko, *Lepidodactylus lugubris*, colonised Heron Island in the southern Great Barrier Reef in 1995. Although isolated individuals of a wide range of non-avian terrestrial wildlife species arrive on the island with cargo, this forested coral cay has no history of a successful colonisation by a terrestrial reptile. This gecko did not originate from the adjacent mainland or from a nearby island. It is likely that the gecko has arrived among a tourist's luggage. ❐ *Lepidodactylus, colonisation, Heron Island, Great Barrier Reef, Queensland, Australia.*

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This study reports the recent colonisation of Heron Island in the southern Great Barrier Reef (GBR) of Queensland by the Mourning Gecko, *Lepidodactylus lugubris,* and discusses the possible source of the founding individual(s). Heron I. is a forested coral cay, approximately 830m long and 300m wide, lying approximately 80km off the coast from Gladstone in the southern GBR. The island was formed from non-terrigenous sediments derived from the surrounding coral reef (Mather & Bennett, 1984). This and neighbouring islands formed when sea levels stabilised after the last Holocene transgression and they have never been connected to the mainland or to each other. There are no non-avian terrestrial vertebrates native to Heron I. or other islands of the Capricorn-Bunker Groups or on Lady Elliott I., another nearby coral cay to the south (Mather & Bennett, 1984). There has been no evidence of aboriginal habitation of these islands since European explorers discovered them in the early 1800s. There is no evidence of terrestrial reptiles native to the island prior to the continual European residency which commenced in 1925 with a turtle soup factory. The island village currently comprises a tourist resort, a research station and the Marine Parks Ranger Station. The discussion explores reasons why this recent colonising event by *L. lugubris* has been successful while other terrestrial reptilian colonisations have failed.

## METHODS

One of us (CJL) has been a frequent visitor to Heron I. (23°26'S 151°55'E) and other islands of the Capricorn-Bunker Groups from 1962 up to the present and has examined the islands intermittently by day and night in search of terrestrial fauna. Geckos were captured by hand and measured (±0.01cm) for snout-vent length (SVL) and tail length from the anterior of the vent, using vernier calipers. SVL and tail length were summed for calculating total length. Each gecko was examined for presence of original or regrowth tail and for presence or absence of enlarged bulges of invaginated hemipenes on each side of the ventral base of the tail. Shelled oviducal eggs, visible through the ventral body wall, were counted. Additional data on the occurrence of the gecko on Heron I. were obtained through interviews with residents and regular visitors to the island. Information on the ports of origin of resort guests was obtained from interviews with management personnel at the resort.

## RESULTS

The earliest records of a gecko resembling *L. lugubris* inhabiting Heron I. date from October 1995 when reports of geckos on the tourist resort buildings were recorded in wildlife sightings log books and a gecko was observed under bark of a dead *Casuarina equisetifolia* on the northern strand in front of the tourist resort (A. Congram, pers. comm.). The first sightings at the Marine Parks Ranger Station occurred in January 1996

(A. Phillott, pers. comm.). During our visit to Heron I. in late October – early November 1996, geckos were found to be common nocturnal foragers on the walls and ceilings of all illuminated buildings of the tourist resort. None was found on unlit buildings, on strand tree trunks or on the research station or Marine Parks buildings during spotlighting searches. Given the number of buildings with the gecko present and the numbers seen on individual buildings, the *L. lugubris* population on Heron I. in November 1996 would have consisted of hundreds of lizards. In August 1997, when the next search was made for the species, it was abundant on the lighted walls of buildings at the tourist resort, research station and Marine Parks base.

A captured sample of 45 *L. lugubris* was examined on 3-4 November 1996. None had enlarged bulges on the ventral base of the tail and all were presumed to be females. The geckos ranged in size from the smallest immature with SVL = 1.91cm (total length = 3.69cm) to the largest adult with SVL = 4.87cm (total length = 9.68cm). Four specimens were lodged in the Queensland Museum collection (QMJ62556-62559).

The smallest gecko with oviducal eggs measured SVL = 4.12cm. If this is taken as the minimum adult size, then there were 30 adult sized geckos. Twenty-five (83%) of them were adults based on the presence of oviducal eggs. Whether the remaining five adult-sized geckos were non-breeding adults or large immature individuals was not determined. Mean size of gravid geckos was SVL = 4.45cm (SD = 0.21, range = 4.12-4.87, n = 25). Of the gravid geckos, 22 (88%) had two oviducal eggs (one egg in each oviduct) and 3 (22%) carried a single oviducal egg. There was no knife-edge effect by size for the presence of oviducal eggs (Figure 1).

The high proportion of original tails within the sample (40/45) suggests that these geckos are not subjected to intense predation. Potential predators on Heron I. would be primarily from the avifauna: reef egret, buff-banded rail and sacred kingfisher. While egrets and kingfishers can be expected to eat any *L. lugubris* encountered by day, only the rails regularly foraged at night when the geckos were also active. However, geckos on walls and tree trunks would be mostly beyond the foraging range of the rails. Large spiders may prey on some very small geckos.

## POTENTIAL SOURCES OF NON-AVIAN TERRESTRIAL INTRODUCTIONS

A wide range of items, including building materials, sand and gravel, food, furniture and machinery, have been shipped weekly to Heron I. from Gladstone on the adjacent mainland for decades. As a result, there has been a considerable potential for local wildlife to be introduced to the island. However, *L. lugubris* is not known from the mainland adjacent to Heron I. Recorded instances of introductions of other species to the island have been relatively infrequent. The introduced rat, *Rattus rattus*, was abundant throughout the island in 1962. Between 1963 and 1967, the rats were eradicated with a baiting program (R. Poulsen, pers. comm.). Heatwole (in Mather & Bennett, 1984) recorded 3 introductions of lizards to the island but identified only the dragon, *Pagona barbatus*. Within two weeks of introduction of roll-on, roll-off barging of cargo in the late 1970s, a *Bufo marinus* was captured on the island. A green tree frog, *Litoria caerulea*, regularly was heard calling from a septic system ventilator over a summer in the early 1990s. In recent years some snakes have been found and immediately killed on Heron I.: an eastern brown snake, *Pseudonaja textilis*, arrived in a palette of equipment in the summer of 1993-1994; a green tree snake, *Dendrelaphis punctulatus*, arrived among building materials during the summer of 1996-1997. In early 1997 a gecko resembling a *Gehyra* ran from a carton of vegetables that had recently arrived from the mainland (E. Grant, pers. comm.). The house mouse, *Mus musculus*, has become established on the island and eliminated by baiting and trapping on several occasions. In August 1997, house mice were common and widespread on Heron I. Human alterations to the island may have on occasions enhanced the survival of species that normally would not have survived for long after their arrival. For example, although not a case of unnatural arrival at Heron I., yellow-bellied sheathtail-bats, *Saccolaimus flaviventris*, had an extended residency on Heron I. in March-April 1992 facilitated by the opportunity to forage each night in the cleared area of the recently constructed open topped sewerage treatment tanks.

Although rodents have colonised other islands within the Capricorn-Bunker Groups (Northwest: *M. musculus*; Wreck: *R. rattus*; Faifax: *R. rattus*.) at various times during this century, there are no previous colonisations of any of the coral cays within a 100km radius of Heron I. by terrestrial

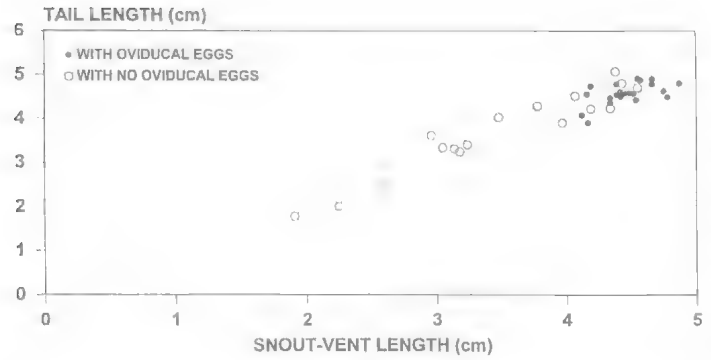



FIG. 1. *Lepidodactulus lugubris* at Heron Island: distribution by size, with and without oviducal eggs.

reptiles except for Wilson I. and Lady Elliott I. One species of terrestrial reptile occurs on Wilson I. (23°18'S 151°55'E), the Asian House Gecko, *Hemidactylus frenatus* (Heatwole, in Mather & Bennett, 1984). *H. frenatus* is not resident on the adjacent mainland or on adjacent islands. It has been a resident of Wilson I. since at least 1977 (CJL unpubl. data). For more than 30 years, the Heron I. tourist resort has conducted regular day visits to Wilson I., ~14km from Heron I. Food, rubbish and other items were repacked at Wilson I. and returned to Heron I. at the completion of each day's visit yet *H. frenatus* has not been recorded on Heron I. Lady Elliott I. (24°07'S,152°43'E) had been colonised by the 1960s by two species of terrestrial diurnal skink ('*Sphenomorphus tenuis*' [=*Eulamprus* sp. Greer, 1992] and *Cryptoblepharus virgatus*) which most probably had been transported to the island via human activities associated with guano mining and the manned lighthouse (Heatwole in Mather & Bennett, 1984). At that time Lady Elliott I. had been deforested and had a depauperate population of egrets, rails and other potential predators of these reptiles (P. Ogilvie, pers. comm.).

Rafting of wildlife to Heron and adjacent islands from the mainland following floods has been rarely observed. In the week following the extensive 1991 flooding of the Fitzroy River, 'small green frogs' were observed on marker buoys and floating hyacinth clumps on the perimeter of Heron Reef and freshwater turtles, *Chelodina longicollis*, came ashore on Heron I. and Northwest I. The latter were collected and returned to the mainland.

There has been an unconfirmed report of the release of geckos on Heron I. as part of a colonisation experiment in the late 1960s or early 1970s. The last sighting of geckos that may have been associated with this were recorded on the research station buildings in 1973. These geckos included a medium sized arboreal species that was most likely a *Gehyra*. Although searches of the island for geckos were made irregularly in the intervening period, no gecko population was found on the island until 1995.

Visitors to the Tourist Resort and Research Station and island residents returning from holidays all bring luggage when they arrive at Heron I. It is not uncommon for some items of luggage, especially dive equipment, to arrive unopened on Heron I. after having been packed at distant sites. Unfortunately, neither the use of colour patterns nor current mtDNA genetic analysis can provide the degree of resolution necessary to identify the site/country of origin for these *L. lugubris* (C. Moritz, pers. comm.). The capacity for this gecko to hitch-hike into new locations is illustrated by a SCUBA diver from the Heron I. tourist resort in September 1997 surfacing after a 30min dive at 10-12m depth on the outside of Heron I. Reef with an adult sized gecko crawling in her hair. The gecko was quite active and was returned to the island and released (E. Grant, pers. comm.). This particular gecko is presumed to have been transported from the island in the diving equipment.

## DISCUSSION

*Lepidodactylus lugubris* occurs widely throughout the Indo-Pacific region in triploid asexually reproducing (parthenogenic) populations (Moritz et al., 1993, Radtkey et al., 1995). The species has been recorded previously from Australia from the islands in Torres Strait, from islands along the inner shelf of the northern Great Barrier Reef to as far south as the Barnard Is (17°40'S 146°11'E, Kluge, 1963) and from coastal mainland sites near Cape York, Portland Roads and the Port Douglas to Mission Beach area (Cogger, 1994; Ingram & Raven, 1991; CJL, unpubl. data). Within this distribution, this gecko appears to inhabit rocks, logs, trees and buildings, including beached boats, in the immediate vicinity of the strand (CJL, unpubl data). The Barnard Is population was first noted by Kluge (1963) on the

basis of two old (probably last century) specimens in the Macleay Museum and reconfirmed in 1969 (Australian Museum specimen, R49919. Glen Shea, pers. comm.). No previous records of *L. lugubris* were obtained from S of Mission Beach (17°56'S, 146°06'E) even though there were extensive searches for this species on islands and in coastal areas between Mission Beach and Townsville during 1976-1979 by Queensland National Parks and Wildlife Staff (CJL, unpubl. data).

The colonisation of Heron I. in 1995 by *L. lugubris* is the first successful colonisation of the island by a terrestrial reptile. Because *L. lugubris* does not occur on the adjacent mainland or nearby islands (Cogger, 1994; Mather & Bennett, 1984), it must have originated from a more distant site. Therefore, it is highly unlikely that the colonising geckos arrived by barge from the mainland. Similarly it is unlikely to have arrived by rafting on floating debris from the sea. It is more likely that the gecko arrived within luggage. As the early records from the island were aggregated within the tourist resort, it is most probable that this was the site of introduction. On the basis of tourist movements there is some probability that it has arrived from a distant Pacific I. site direct to Heron I. rather than from N Queensland, although the latter cannot be discounted. Being a parthenogenic species, it would be possible for the arrival of a single individual of *L. lugubris* to result in the establishment of the present expanding colony. The greater abundance of individuals in association with illuminated buildings is consistent with *L. lugubris* habitat usage on inhabited islands elsewhere in the Pacific (Petren, 1993). Indeed, the regular presence of small insects around these lights at night may have enhanced the survival of the gecko on Heron I. Whether the distribution of *L. lugubris* to as far south as the Barnard Is is natural or resulted from the extensive movement of fishing boats between islands of the northern Great Barrier Reef and Torres Strait during the 1800s is conjectural. In contrast, the Heron I. *L. lugubris* population clearly has arrived by anthropogenic means and represents an ~850km extension of range south of Mission Beach.

That terrestrial wildlife invades Heron I. via the materials and equipment brought to the island from Gladstone and other areas, is not surprising. What is surprising is that, apart from rodents, no non-avian vertebrates have successfully colonised Heron I. prior to this colonisation by *L. lugubris*. There is a range of genera of small skinks and geckos (*Carlia, Cryptoblepharus, Ctenotus, Lamphropholis, Gehyra, Heteronotia*) with species that occur in the coastal area of Gladstone and which, should they arrive at Heron I., could be expected to successfully colonise the island (in fact, a specimen of *Carlia schmeltzii* was collected in the tourist resort at Heron I. in 1998 by A. Congram). However, the abundance of terrestrially foraging, carnivorous/insectivorous avifauna such as egrets, rails and kingfishers may have a significant impact on survival of ground dwelling or diurnal species when they periodically arrive on Heron I. For sexually reproducing species, there is the additional limitation of multiple individuals of both sexes having to be present on the island at the same time. Other forested Capricorn-Bunker islands such as North West I., Wreck I., Fairfax I. and Lady Musgrave I. have a history of decades of human habitation and visitation and an abundance of reef egrets and landrails and kingfishers. The first three of these islands have been colonised by rodents but not by terrestrial reptiles.

The two reptiles that have colonised Capricorn-Bunker islands have been small, parthenogenic, nocturnal, arboreal geckos, *L. lugubris* on Heron I. and *H. frenatus* on Wilson I. Both species have a well established history of colonising new locations by traveling with people. In contrast, Lady Elliott I., a coral cay to the south of the Capricorn-Bunker Groups, was colonised by two species of small non-parthenogenic, terrestrial to partially arboreal, diurnal reptiles (Heatwole in Mather & Bennett, 1984). However, this island had been highly modified with an almost complete loss of trees since last century and, as a result, supported a depauperate population of egrets, rails and other potential predators of these reptiles (P. Ogilvie, pers. comm.). The characteristic avifauna of these forested coral cays of the southern Great Barrier Reef and the absence of reptile species living on the adjacent mainland that possess the suitable suite of coloniser characteristics (small, parthenogenic, nocturnal and aboreal) are presumed to have contributed to the restricted colonisation of the forested islands by terrestrial reptiles. That there is an element of randomness to colonisation events such as this is emphasised by the arrival of *L. lugubris* from a distant site rather than *H. frenatus* colonising Heron I. from nearby Wilson I.

## ACKNOWLEDGEMENTS

Department of Environment staff (A. Congram, A. Hollis), Heron I. resort staff (S. Noonan, E. Grant, M. McKillop) and A. Phillott shared their observations of wildlife at Heron and adjacent islands. S. Noonan and L. Grant provided information of the movement patterns to the island for resort staff and guests. P. Ogilvie provided helpful comments during preparation of the manuscript. G. Shea and an unnamed person provided a constructive review of the manuscript. This assistance is gratefully acknowledged.

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**RANGE EXTENSION FOR THE INTRODUCED BLIND SNAKE, *RAMPHOTYPHLOPS BRAMINUS* (TYPHLOPIDAE) IN QUEENSLAND.** *Memoirs of the Queensland Museum 43(2): 782. 1999:-* The typhlopid snake *Ramphotyphlops braminus* has a wide distribution in tropical and subtropical regions of the world. It is Australia's only introduced snake, and the 2 known populations in Darwin (NT) and Torres Strait (Qld) probably arrived from SE Asia in cargo (Wilson & Knowles, 1988). *Ramphotyphlops braminus* is an efficient disperser because it is closely associated with humans, is frequently transported in cargo, and is parthenogenetic (McDowell, 1974). Here we report a population of *R. braminus* from Townsville, N Queensland (19°17'S 146°47'E).

On 3 October 1998, a specimen (QMJ67248) was collected under a flowerpot in the Townsville suburb of Heatley (Fig. 1). On 10 October 1998, a second specimen (QMJ67249) was accidentally killed in the same garden, and on 24 October 1998, 2 additional specimens were collected from beneath flowerpots in this garden. Another specimen collected from the Townsville suburb of Condon on 21 October 1998, has been deposited with the Queensland Department of Environment and Heritage.

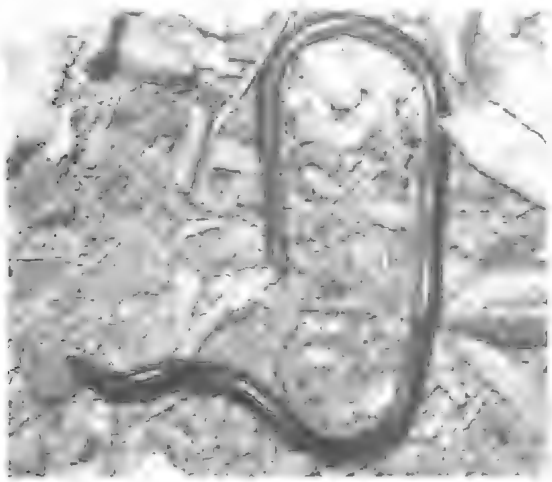


FIG. 1. *Ramphotyphlops braminus* from Townsville, NE Queensland.

The Townsville specimens are identified as *R. braminus* and distinguished from all other Australian typhlopid snakes (Cogger, 1992) by the following combination of characters: small and slender (<150mm total length); midbody scales 20; nasal cleft joining preocular; head scales with numerous tiny tubercles; prominent whitish glands between head scales. In life dark purplish brown dorsally grading to pale brown ventrally. In preservative dark chocolate brown dorsally grading to pale brown ventrally, anterior edges of scales darker brown. Chin, cloaca and tail spine white.

These records represent a large range extension for this species, and only the third known population in Australia. The close association with suburban gardens, and in particular with flowerpots, is typical of this species. The population is almost certainly a recent arrival. This is the first record of this species from the Heatley locality, where the senior author has resided for 10 years.

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# FIRST PLIOCENE RECORD OF THE MADTSOIID SNAKE GENUS *YURLUNGGUR* SCANLON, 1992 FROM QUEENSLAND

B.S. MACKNESS AND J.D. SCANLON

Mackness, B.S. & Scanlon, J.D. 1999 06 30: First Pliocene record of the madtsoiid snake genus *Yurlunggur* Scanlon, 1992 from Queensland. *Memoirs of the Queensland Museum* **43**(2): 783-785. Brisbane. ISSN 0079-8835.

A single, large snake vertebra was recovered from a quarry in Chinchilla, southwestern Queensland. Its description is consistent with *Yurlunggur* and confirms that this genus persisted beyond the Miocene in Australia. ❐ *Yurlunggur, Matsoiidae, Pliocene.*

*B.S. Mackness & J.D. Scanlon, School of Biological Sciences, University of New South Wales, Sydney 2052, Australia; 10 November 1998.*

Four species of madtsoiid have been reported from the Cainozoic fossil record of Australia; *Wonambi naracoortensis* Smith,1976 (Pleistocene), *Yurlunggur camfieldensis* Scanlon, 1992 (Miocene), *Patagoniophis* sp. cf. *P. parvus* Albino, 1986 and *Alamitophis* sp. cf. *A. argentinus* Albino, 1986 (Scanlon 1993, Eocene). The last mentioned is the oldest known snake from Australia. Madtsoiids are closely related to South American specimens from the Late Cretaceous (Scanlon 1993). Outside Australia, madtsoiids did not survive beyond the Eocene (Rage, 1987). In Australia, Pleistocene to Pliocene records of madtsoiids have been referred mostly to *Wonambi naracoortensis* or cf. *W. naracoortensis* (see Merrilees, 1979; Flannery, 1989; Barrie, 1990; McNamara, 1990; Pledge, 1992). Scanlon (1995) reported *W. naracoortensis* from an additional Pleistocene locality (Wellington Caves, New South Wales), but also suggested that species of *Yurlunggur* may have been present in either or both the Curramulka Local Fauna (probably early Pliocene, S South Australia, Pledge, 1992) and the Wyandotte Local Fauna (NE Queensland, McNamara, 1990). The specimen described here confirms the interpretation that *Yurlunggur* persisted beyond the Miocene.

A single large snake vertebra was recovered during quarrying operations at the Rifle Range at Chinchilla, SW Queensland. The fossil comes from a sandy sequence of fluviatile deposits known as the Chinchilla Sand (sensu Woods, 1960), interpreted as middle Pliocene age based on biocorrelation with the Bluff Downs Local Fauna (Archer, 1976). A number of other large snake vertebrae have been reported from the Bluff Downs (Mackness, 1995) and also the Spring Park Local Faunas (Mackness et al., 1993) but these are all pythonines. This paper reports the first ophidian fossil from the Chinchilla Local Fauna as well as the first record of the Madtsoiidae from the Pliocene of Queensland.

Terminology for the vertebra follows Auffenberg (1963), Hoffstetter & Gasc (1969) and LaDuke (1991). A cast of the vertebra is registered in the Queensland Museum (QMF30560).

## SYSTEMATICS

### Family Madtsoiidae Hoffstetter, 1961

### **Yurlunggur** sp. Scanlon, 1992

(Fig. 1)

The vertebra is referred to the Madtsoiidae because it has the following combination of characters: prezygapophyseal processes absent, zygapophyses inclined well above horizontal, paradiapophyses extend laterally beyond prezygapophyses, paracotylar and parazygantral foramina present. It is referred to *Yurlunggur* because of a moderate slope of the zygapophyses (<22° above horizontal) and strong overall resemblance to vertebrae of *Y. camfieldensis* Scanlon, 1992.

DESCRIPTION. The specimen is a large trunk vertebra, lacking any of the specialised processes that characterise other regions of the column. The anteroposteriorly short centrum and single hypapophysis indicate a position in the anterior portion of the trunk. It is complete except for the distal part of the neural spine and slight damage to the postzygapophyses.

The centrum is broadly triangular in ventral view, the ventral face strongly defined by subcentral ridges converging posteriorly towards the condyle at nearly 90° from each other. A narrow

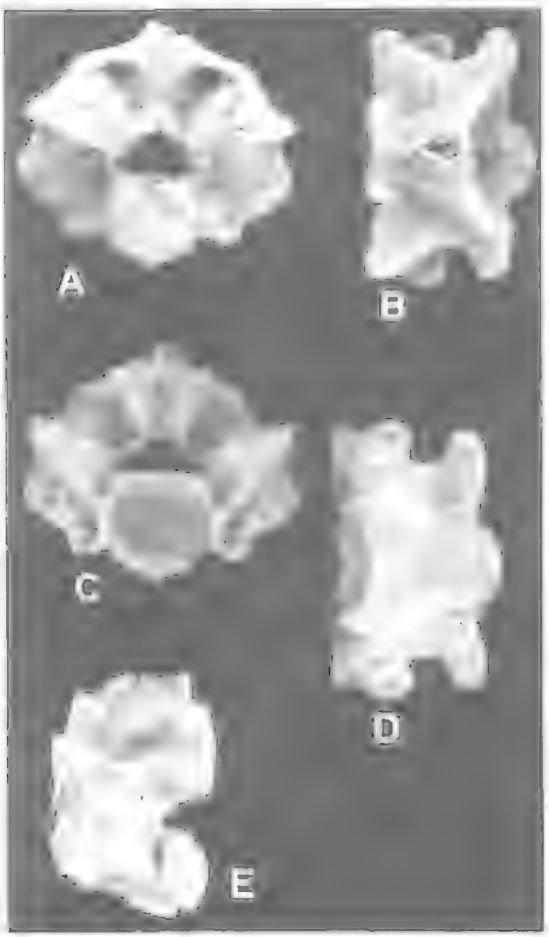



FIG 1. Vertebra of *Yurlunggur* sp. in A, posterior; B, dorsal; C, anterior; D, ventral and E, lateral views. Actual size.

but not very prominent hypapophysis is present on the posterior half of the centrum, with only a low ridge (between shallow ventrolateral concavities) extending to the cotylar rim. In lateral view, the hypapophysis is defined by a very distinct 'step' anteriorly and is nearly horizontal ventrally. It is sharp and narrow anteriorly, but thickened posteriorly by lateral ridges (incipient paired hypapophyses). Hypapophyses of similar form occur in the posterior precardiac region (transition to 'mid-trunk') of *Yurlunggur* spp. (*Y. camfieldensis*, Scanlon, 1992, fig. 1B,C), but are not known in *Wonambi*.

Zygapophyses are inclined at about 20° above the horizontal, their planes intersecting at the base of the neural canal. Zygapophyseal facets are obovate but slightly pear-shaped, distal parts slightly distinguished by anteroposterior constrictions and prominent growth rings which are likely to reflect individual variation (perhaps an interruption of growth due to seasonal variation or injury). Long axes of the prezygapophyses are transverse, postzygapophyses extending slightly posteriad. Interzygapophyseal ridges are smoothly concave laterally.

Zygosphene about the same width as cotyle, and about as deep as wide. Zygosphenal facets slightly concave laterally, diverge dorsally at about 30° from vertical, and their tangental planes intersect between the centre and base of the neural canal. Neural canal weakly trifoliate, slightly wider than high. Zygosphene roof arcuate in anterior view, neural spine extending as a low, dorsally concave crest almost to the anterior edge. This differs from *Wonambi* where the spine rises steeply from the middle of the zygosphene roof, and from most *Yurlunggur* where it is almost entirely posterior to the zygosphene. Spine is broken, so that its original height is unknown, but was steeper and probably higher than in *Y. camfieldensis*.

Paradiapophyses extend slightly beyond the prezygapophyses laterally. In lateral view, they are kidney-shaped, slightly indented posteriorly, but without the strong dorsal concavities of *Wonambi* (Scanlon 1995). Paracotylar, parazygantral, zygantral, and upper and lower lateral foramina present: two or three small subcentral foramina on each side rather than the usual large pair.

The specimen is somewhat smaller than the most similar vertebrae in *Yurlunggur camfieldensis* holotype, and thus represents a smaller individual; centrum relatively shorter and condyle more depressed and oblique, consistent with size differences being ontogenetic (with the usual allometry) rather than difference in adult size. Apart from slight proportional differences, the greatest difference from *Y. camfieldensis* (Scanlon, 1992, fig. 1B) is the more elevated neural arch, in posterior view sloping gradually up to the neural spine rather than forming a horizontal roof over the zygantrum.

Measurements (mm) of *Yurlunggur* sp. vertebra: zygosphene width 13.5; zygosphene height 8.2; neural canal height 4.5; zygantrum width 15.6; paradiapophysis width 34.7; paradiapophysis internal width 19.7; condyle width 12.3; prezygapophysis width 32.9; pre/postzygapophysis length 19.5; centrum midline length 14.0.

This specimen further extends the known geographic and temporal range of *Yurlunggur* in

Australia. Although originally described from the Middle Miocene of the Northern Territory, the genus has also been reported from the Late Oligocene to Middle Miocene of Riversleigh, NW Queensland (Scanlon, 1992), and apparently persisted in northern Queensland until the Late Pleistocene (Scanlon, 1995).

Remains of large pythons and large madtsoiids have been found together but with different frequencies in deposits at Riversleigh and Bullock Creek (Smith & Plane, 1985; Scanlon, 1992) suggesting ecological differences (Scanlon, unpubl. data). Very large pythonine snakes are also known from the Pliocene of N Queensland (Archer, 1976; Mackness et al., 1993; Scanlon & Mackness, unpubl. data) but so far there is no evidence of sympatry between madtsoiids and pythons later than the Miocene (Scanlon, 1995). Whether the extinction of madtsoiids can be attributed to direct competition from pythons is thus doubtful.

## ACKNOWLEDGEMENTS

The authors thank Sandra Clark who recovered the vertebra, and Cec and Doris Wilkinson, Chinchilla who brought the specimen to our attention.

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**CARBONIFEROUS FISH REMAINS FROM THE FAR-NORTHERN DRUMMOND BASIN.** *Memoirs of the Queensland Museum 43(2): 786. 1999:-* The Drummond Basin has yielded modest Carboniferous fish faunas (e.g. Turner, 1993; Fox et al., 1995), but these have been restricted to the central and southern parts of the basin. More recently the discovery of tetrapod material (Thulborn et al., 1996) has intensified the basin-wide search for vertebrate fossil sites which could be of significance in understanding the early evolution of terrestrial and freshwater vertebrates in eastern Gondwana.

We here report the occurrence of a small fossil fauna from the Bulliwallah Formation, near Plain Creek, 23°33.04'S, 146°29.95'E, NW of Belyando Crossing, CEQ (=QML1156). The Bulliwallah Formation is regarded as a freshwater deposit and has been assigned a Visean age (Olgers, 1972) and is thought to be equivalent to the Ducabrook Formation (Tweedale, 1960). This site is significant in that it contains the first Palaeozoic non-marine vertebrates preserved in nodules, and it is of similar age to fossil localities to the south containing tetrapod remains.

Material from this site is preserved in buff-to orange-grey claystone nodules, which were dredged from an earth dam during construction. The fauna includes a large spine of *Gyracanthides* sp. (Fig. 1), ?*Acanthodes* (QMF39822, spines and scales) and palaeoniscoid remains (QMF39823, possible skull fragments).

**Acknowledgements**

We thank Reid Russell of Plain Creek for bringing this material to our attention and kindly donating it to the Museum.

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*Susan Turner & Alex G. Cook, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 6 November, 1998.*

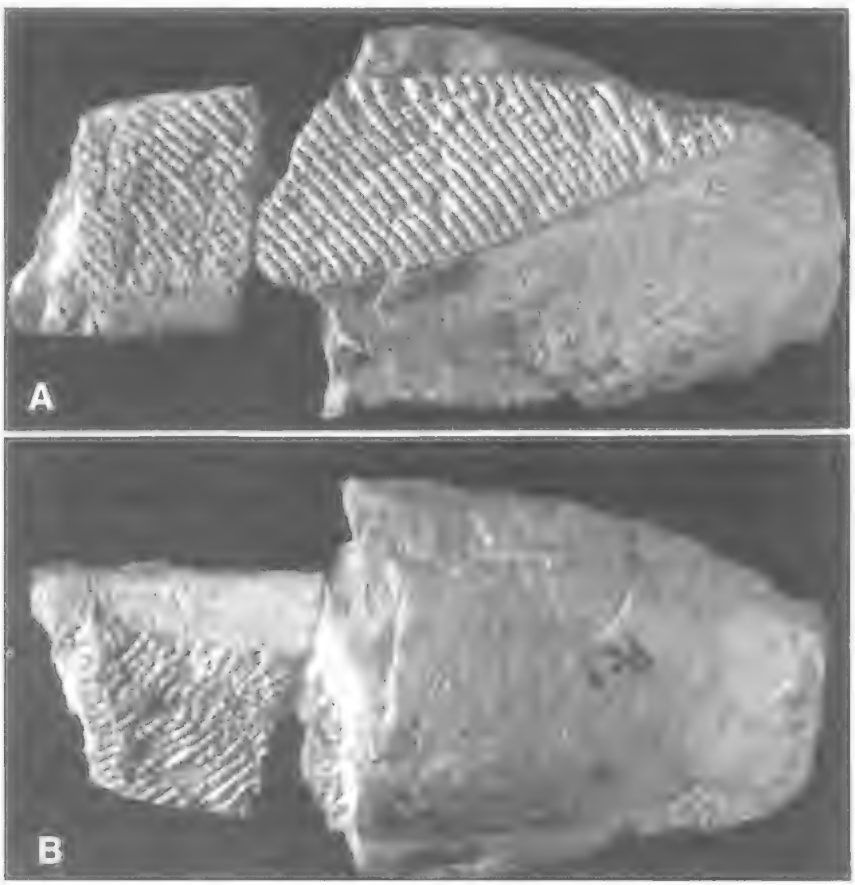



FIG. 1. A, B. *Gyracanthides* sp., spine, QMF39821, ×32.

# ACTINOPTERYGIANS FROM THE EARLY TRIASSIC ARCADIA FORMATION, QUEENSLAND, AUSTRALIA

CAROLINE NORTHWOOD

Northwood, C. 1999 06 30: Actinopterygians from the Early Triassic Arcadia Formation, Queensland, Australia. *Memoirs of the Queensland Museum* **43**(2): 787-796. Brisbane. ISSN 0079-8835.

Isolated scales and small patches of articulated scales, collected as surface scrap, provide evidence of 6 additional types of actinopterygian from the Arcadia Formation. Prior to the description of these scales, *Saurichthys* was the only actinopterygian known from the Arcadia Formation and as none of the scales are referable to this genus, they significantly increase the faunal diversity of the collections. ❐ *Actinopterygians, Arcadia Formation, Queensland, Australia.*

*Caroline Northwood, Department of Zoology, La Trobe University, Bundoora 3083, Australia; 5 October 1998.*

Exposures of the Arcadia Formation are seldom fossiliferous but there are two localities where the sediments erode to form natural craters in which vertebrate fossils become concentrated. Assemblages accumulated over a 30-year period, mostly of surface scrap, are dominated by the remains of temnospondyl amphibians, with procolophonids, basal archosaurs and other small reptiles present in small but significant numbers. Lungfish toothplates are also common. Actinopterygian remains are rare, except as inclusions in coprolites, which occur in abundance (Northwood, 1997). The only actinopterygian previously recorded from the assemblages is *Saurichthys* cf *S. gigas* (Turner, 1982).

It is clear from the frequency of coprolites containing scales that actinopterygians were important members of the community represented in the Arcadia Formation. Unfortunately, most of the scales in the coprolites are too poorly preserved to be described. Instead, an idea of the diversity of actinopterygians present can be gained by studying scales preserved in small pieces of matrix collected with the surface scrap. Some of these scales are reasonably well preserved and remain articulated. Others are scattered through small pieces of fine sandstone or mudstone and vary in their quality of preservation. Variations in morphology and surface ornamentation allow different types of actinopterygians to be recognised.

The scales described here are from two sites, Queensland Museum Locality (QML) 78 (the Crater), which lies approximately 72km SW of Rolleston, and QML215 (Duckworth Creek), situated SW of Bluff, both in S central Queensland, and approximately 175km NNE of QML78. Sediments at the two localities are derived from high-sinuosity, meandering to anastomosing streams subject to frequent seasonal flooding. Thick successions of massive purplish-red overbank mudstones enclose well defined channel sandstones which are whitish-green, fine to medium grained, and cross-bedded. Channel deposits are more abundant at QML215 than at QML78. Flash floods are represented by thin bands of massive to weakly laminated, whitish-green mudstone and very fine sandstone interbedded with red mudstone. Vertebrate fossils are recovered mostly from the fine grained sediments, but isolated elements are recovered occasionally from the more coarse grained sandstone. Most of the actinopterygian scales are enclosed in fine to medium-grained red matrix, which suggests preservation in interchannel mudstones, probably on mud flats. At QML215 some specimens are preserved in green mudstone thought to have been deposited in a swampy environment (Northwood, 1997).

Scales described in this paper are divided into six types representing different actinopterygian taxa, all of which are new for the Arcadia Formation. Comparisons are made with scales from other Early Triassic actinopterygians from Australia and South Africa. Two main problems were encountered during this analysis. First, there seems to be a preservational bias against fish in most Early Triassic non-marine deposits that limits the available comparative material. Secondly, the scales of those actinopterygians which are known from the Early Triassic are incompletely preserved or not described in detail.

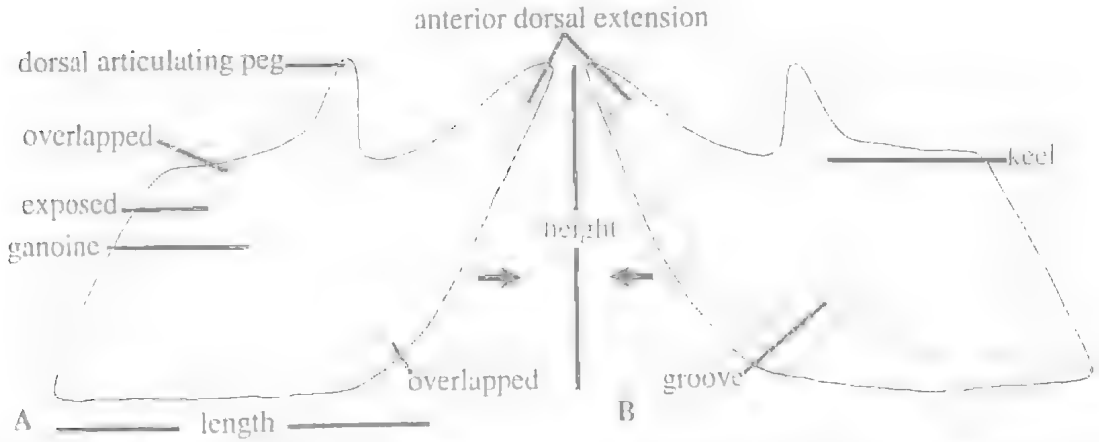



FIG. 1. Morphological features of Early Triassic actinopterygian scales and the terminology used to describe them. A, external view; B, internal view; arrow = anterior.

The Australian actinopterygians are no exception. Despite these problems, the comparisons indicate that some of the Arcadia scales may belong to members of the Aerolepidae and Perleididae.

## MORPHOLOGICAL CHARACTERISTICS OF ACTINOPTERYGIAN SCALES

Characteristically, most Early Triassic actinopterygians have ossified scales with thick laminated ganoine on their exposed surface. The morphological features of actinopterygian scales and the terminology used here to describe them are shown in Figure 1.

The scales of early actinopterygians differ in morphology according to body region (Fig. 2). In general, the scales decrease in height and increase in length toward the caudal, ventral and dorsal regions of the body (Esin, 1990). In the mid-lateral area, the scales are quadrangular, and those nearer the tail are more diamond shaped and less overlapped. Peg-and-groove articulation is reduced or absent in the posterior body scales. Ventral scales tend to be narrow and elongated with a large overlapped area anteriorly (Esin, 1990). This morphological variation of body scales is not great enough to allow the different types of scales from the Arcadia Formation to be from a single taxon.

Esin (1990) observed that other difficulties with using isolated scales for taxonomic purposes are that scales change during ontogeny, and that there is substantial parallelism in the scale morphology of various groups of actinopterygians.

## DESCRIPTION

### TYPE 1.

MATERIAL. QMF35237 (Fig. 3), a single posterior flank scale, preserved in external view in consolidated red mudstone. Locality. QML215.

Scale type 1 is delicate, with a smoothed rhombic shape (Fig. 3). It has a prominent dorsal peg and the anterodorsal corner of the scale extends dorsally beyond the peg. The ganoine layer is thin and the scale is not ornamented. The height and length of the scale are roughly equivalent.

### TYPE 2.

MATERIAL. QMF35238 (Fig. 4A,B,C), anterior - mid lateral body scales, some of which remain articulated, in a small block of red mudstone. Locality. QML215.

Material probably referrable to type 2: QMF35251 from QML215 and QMF35252 from QML78.

Type 2 scales are large, thick, and robust (Fig. 4). The external surface is unornamented and is covered with thick multi-layered ganoine. Dorsally, a prominent peg articulates with a deep ventral groove in the adjoining scale (Fig. 4B,C). Scale type 2 has an extension of the anterodorsal corner, similar to that of scale type 1. On the internal surface of the scale, there is an obvious keel and a depressed area into which the anterodorsal extension of the adjacent scale fits (Fig. 4B). Similar scales have been found at both QML215 and QML78 but are not so well preserved.

### TYPE 3.

MATERIAL. QMF35239 (Fig. 5A), articulated caudal scales, including the lateral line series, in red mudstone.

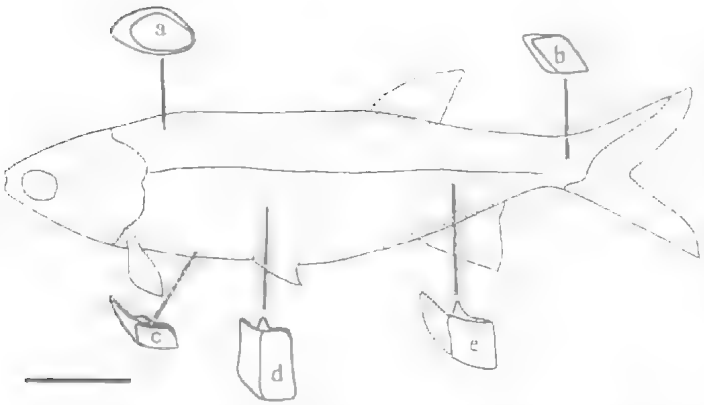



FIG. 2. Morphological variation of scales in the body of a generalised Early Triassic actinopterygian. Dot-shaded areas sometimes have specialised scales, but these were not included as they vary in form between different actinopterygians with less consistency than the other body scales. Scales are adapted from Esin (1990), who figured scales from the different body regions of *Amblypterina costata*. a = anterior dorsal scale, b = caudal scale, c = anterior ventral scale, d = lateral scale, e = posterior flank scale. Scalebar a-e = 5mm; outline of the fish is not drawn to scale.

Only the external surface is exposed. Additional material: QMF35253 (Fig. 5B), scales and lepidotrichia scattered throughout a block of red mudstone that may be a partly decomposed coprolite. Locality. QML78.

The external surface of scale type 3 is ornamented with 3 - 4 rugae that run diagonally across the scale from below the anterodorsal corner to the posteroventral corner (Fig. 5A). There is a slight extension of the anterodorsal corner of the scale which gives it a leaf-like shape. It is a very small, delicate scale with no articulating peg or groove. Often, only the trunk scales of Early Triassic actinopterygians are connected by a peg-and-groove arrangement and the absence of these features in scale type 3 may simply reflect the posterior body position of the scales. The internal surface of scale type 3 has a slight keel and a marginally depressed area where the adjacent scale overlapped (Fig. 5B). Articulated scales show only a slight degree of imbrication.

TYPE 4.

MATERIAL. QMF35240 (Fig. 6A), articulated mid-body scales, including the lateral line series, in a small block of red mudstone. Locality. QML78. Additional Material: QMF35254, 35255, 35256 from QML78 and QMF35257, 35258 (Fig. 6B,C) and 35259 from QML215. At QML78 the scales occur in pieces of consolidated red mudstone with one, QMF35256, occurring in green mudstone.

The actinopterygian represented by scale type 4 is characterised by lateral body scales that are at least 3 times greater in height than length (Fig. 6). The lateral-line crosses the upper quarter of the scales obliquely (Fig. 6A,C). Unlike most of the scale types, type 4 has been collected at both localities, and occurs only as articulated patches of scales. Most of the type 4 scales are poorly preserved and often only the ganoine layer remains. Thus it is unknown whether these scales have a peg-and-groove articulation

Type 4 scales from L215 are less well preserved than those from QML78 and most are little more than impressions in green mudstone. Some of the specimens from QML215 include fin lepidotrichia and lateral-line scales (Fig. 6B,C). Others include the dorsal and ventral margins of the body, where the elongated flank scales grade into smaller, rhombic scales.

TYPE 5.

MATERIAL. QMF35241 (Fig. 7), an articulated patch of mid-posterior flank scales, including the lateral line series, in consolidated red mudstone. Additional material. QMF35260. Locality. QML215.

Type 5 scales are rhombic with no evidence of a peg-and-groove articulation (Fig. 7). In general, the height of the scales is slightly greater than their length (Fig.7A), except for the lateral-line scales which are twice as high as they are long (Fig. 7B). The lateral-line scales have a characteristic notch in the posterior edge and a

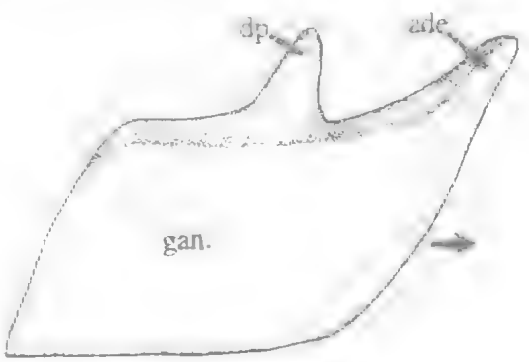



FIG. 3. Scale type 1, QMF35237, posterior flank scale in external view. ade = anterodorsal extension, dp = dorsal peg, gan. = ganoine. Arrow = anterior. Scalebar = 1mm.

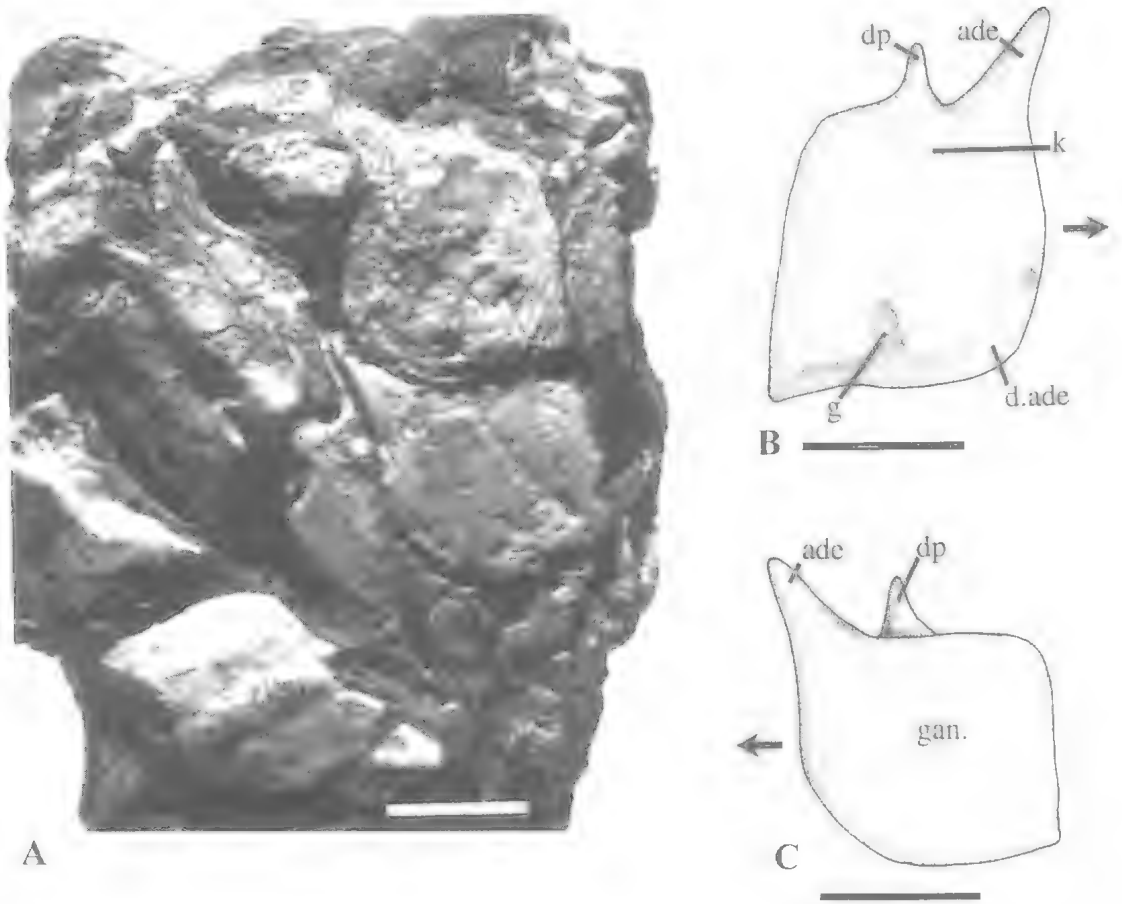



FIG. 4. Scale type 2, QMF35238, anterior - mid lateral scales, some of which remain in articulation. A, QMF35238; B, internal view of a single scale; C, external view of a single scale. ade = anterodorsal extension, d.ade = depression for the anterodorsal extension of the adjacent scale, dp = dorsal peg, g = groove, gan. = ganoine, k = keel. Arrow = anterior. Scalebar = 4mm.

low ridge crossing their external surface, indicating the position of the lateral line.

TYPE 6.

MATERIAL. QMF35242 (Fig. 8), incomplete scales scattered through a piece of consolidated red mudstone. Locality QML215.

Scale type 6 is known from a scattering of incomplete scales of which only the internal surface is exposed (Fig. 8). With no extension of the anterodorsal corner, the scales appear almost square and have a long, pointed peg with an opposing deep, triangular groove. A keel along the centre of the scale is present, but not pronounced. There are a number of small, regularly spaced, ventrally sloping projections along the posterior margin of the scale. One scale has at least 5 projections, but because the scales are incomplete it is difficult to know the number of projections that may have been present originally, or whether the number of projections varied between scales. The matrix also contains a large scale with a fold along the midline that may be an enlarged ridge scale from the dorsal or ventral margin of the tail.

## COMPARISONS BETWEEN THE SCALES

Scale type 1 has a thin, delicate structure that distinguishes it from scales of type 2, which in contrast are robust with several clearly defined layers of ganoine. The rhombic shape of scale type 1 distinguishes it from scale types 4 and 6. The presence of a well-defined dorsal peg and an extended anterodorsal corner distinguish it from

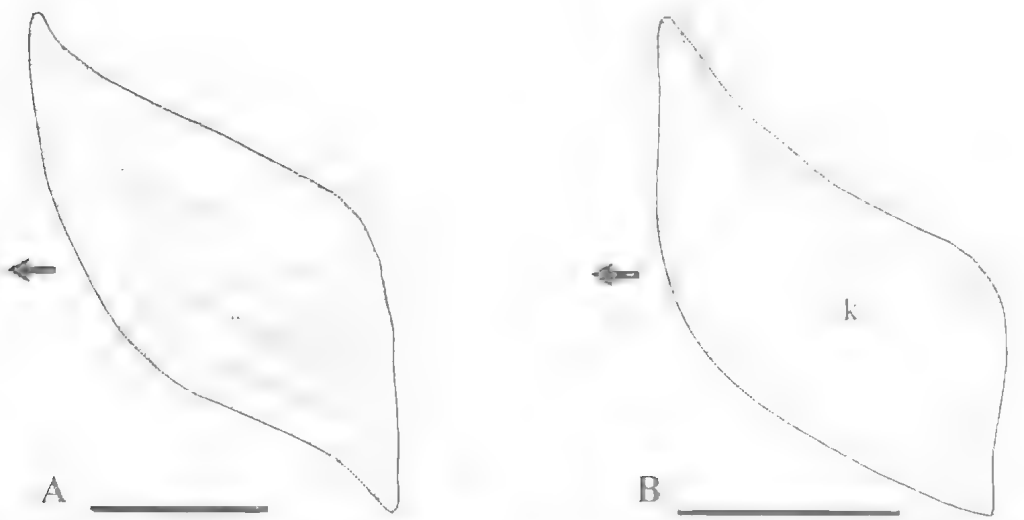



FIG. 5. Scale type 3. A = reconstruction of the external view of a posterior flank or caudal scale from QMF35239, showing the pattern of ornamentation. B = the internal surface of a complete scale from QM F35253, showing the keel. k = keel. Arrow = anterior. Scalebar = 1mm.

scale type 5 and the absence of ornamentation distinguish it from scale type 3.

Type 2 scales can be distinguished from the other Arcadia Formation scales by their larger size, more robust structure, their angular, rhomboid shape, and well developed peg-and-groove articulation.

Esin (1990) found that caudal scales were not useful taxonomically, but the presence of ornament on scale type 3 clearly distinguishes it from the rest of the Arcadia Formation actinopterygian scales, which are unornamented.

The height-length ratio of type 4 scales, in particular the lateral-line series, differentiates them from the other scale types.

Type 5 scales bear some similarity to the more dorsal or ventral scales of scale type 4, where the long body scales grade into more rhomboid scales. The height of the type 5 scales is slightly greater than their length as is the case in scales of type 4. The main difference between the scales of type 4 and type 5 lies in the morphology of the lateral-line scales. In type 4, the lateral line scales are elongate in comparison to the other body scales, whereas in type 5, the lateral line scales do not differ markedly in proportions from the other scales (Fig. 7). Type 5 scales may represent caudal or posterior body scales of the actinopterygian represented by type 4 scales, but it is more likely that differences in morphology of the lateral line scales indicate that type 4 and type 5 scales are from different actinopterygian taxa.

Scale type 6 may be differentiated from the other types of scales described above by its squarish shape, long pointed dorsal peg and deep triangular groove, reduced keel, absence of an extension of the anterodorsal corner, and a characteristic row of ventrally sloping projections along the posterior margin.

## COMPARISONS WITH THE SCALES OF OTHER ACTINOPTERYGIANS

Dziewa (1977) noted that fish faunas from nonmarine environments are dominated by endemic forms. This means that the likelihood of finding actinopterygians with scales that are similar to those from the Arcadia Formation decreases with distance. Accordingly, I only reviewed descriptions of the scale morphology of Early Triassic non-marine actinopterygians from Gondwana.

The Arcadia Formation 'red beds' are typical of many Permian and Triassic deposits in that they show a taphonomic bias against fish and invertebrates while preserving the remains of tetrapods and coprolites in abundance. Fish are likewise rare in most of the other Australian Early Triassic deposits, with the exception of the Terrigal Formation (Gosford Subgroup, Narrabeen Group). This formation has yielded actinopterygian remains in abundance, particularly from the Railway Ballast Quarry and the Somersby Quarry, near Gosford in the Sydney Basin (Kemp, 1994; Ritchie, 1981, 1987; Wade, 1935,

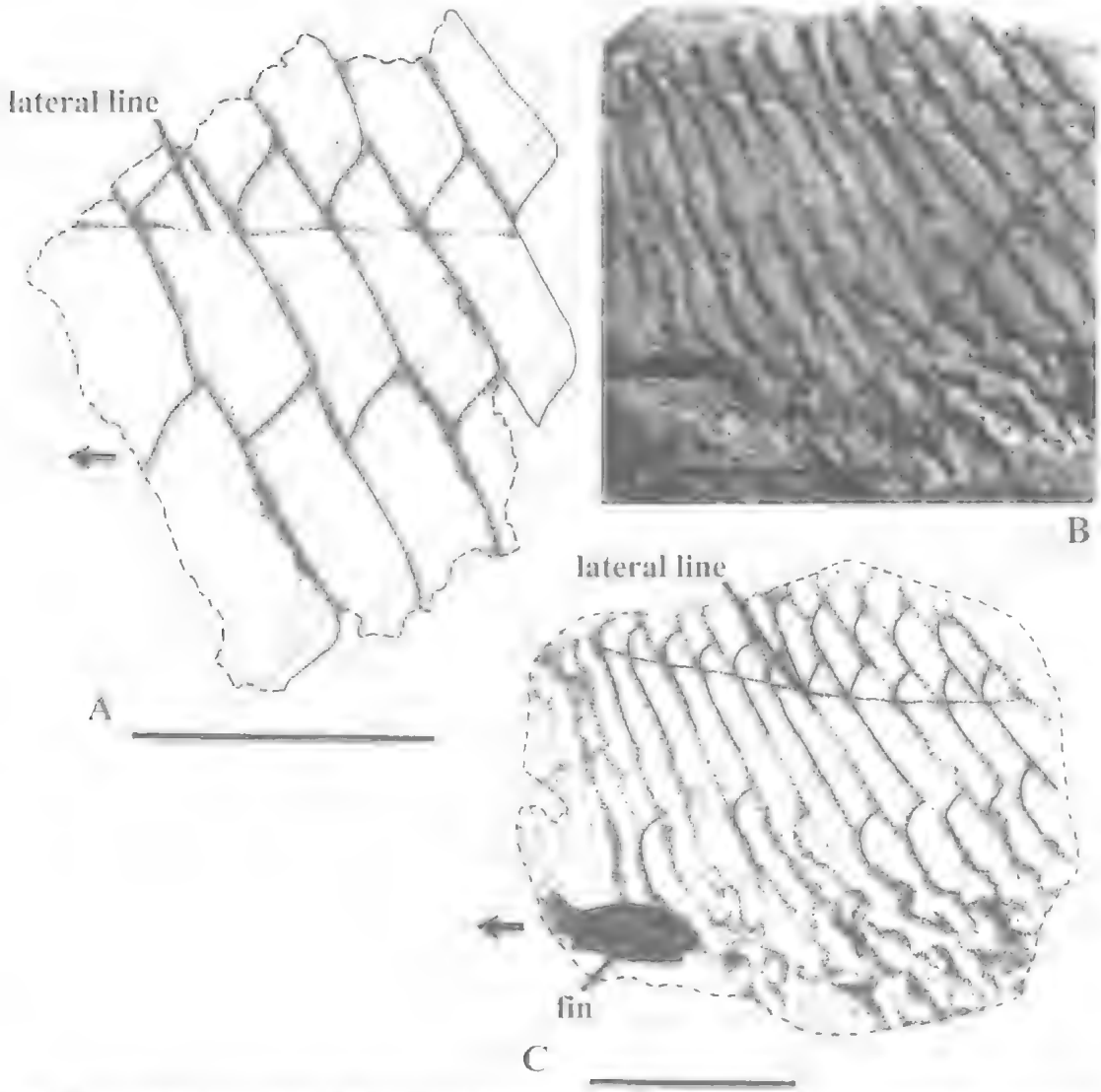



FIG. 6. Scale type 4, articulated scales from the mid body area including the lateral line series. A, reconstruction of QMF35240, showing position of the lateral line and pattern of imbrication; scalebar = 5mm. B, QMF35258, only an impression remains of the scales; scalebar = 5mm. C, QMF35258, showing the lateral line and the impression of a fin. Note the lateral line passes across the upper quarter of the scales in both specimens. Arrow anterior.

1940; Woodward, 1890, 1908). Actinopterygians have also been described from the Knocklofty Formation in Tasmania (Banks et al., 1978; Dziewa, 1977, 1980; Johnston & Morton, 1890, 1891). Unfortunately, the taxonomic status of many Australian Triassic fish is uncertain because cranial regions are usually preserved poorly (Long, 1991).

Actinopterygians are also abundantly preserved in the Bekkers Kraal locality, Orange Free State, South Africa. Unfortunately, the Bekkers Kraal locality and the Gosford quarries are considered to be coeval with the South African Cynognathus Zone fauna and are thus younger than the Arcadia Formation. The Knocklofty Formation is the only Gondwanan deposit, contemporaneous with the Arcadia Formation, to have yielded some reasonably well preserved actinopterygian fossils.

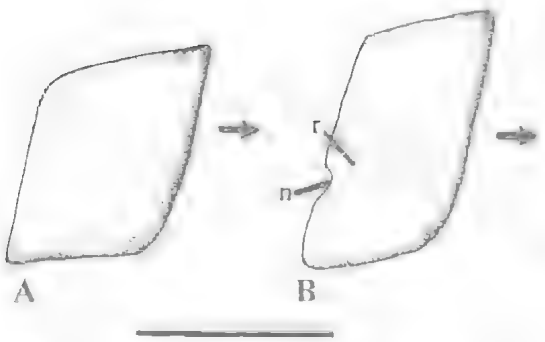



FIG. 7. Scale type 5, QMF35241, articulated mid-posterior flank scales, including the lateral line series. Diagrammatic representation of 2 scales: A, a scale from the series immediately above the lateral line; B, a lateral line scale. Note the characteristic notch in the posterior edge of the lateral line scale. n = notch, r = ridge along the lateral line. Arrow = anterior. Scalebar = 2mm.

Scale types 1 and 2 show a very basic palaeoniscoid pattern that means they compare closely with the scales of many other actinopterygians. Because of this similarity they may not be attributed to any of the described Early Triassic fish.

A characteristic feature of scale type 3 is its ornament. In general, ornament is reduced on the posterior body scales of early actinopterygians and disappears from the caudal scales, but Esin (1990) noted that it remained visible in these areas in two species of *Acrolepis* (*A. rhombifera* and *A. macroderma*). In addition, ornament is present on the caudal scales of the two species of *Acrolepis* from Tasmania (*A. hamiltoni* and *A. tasmanicus*). According to the reconstruction and description provided by Dziewa (1977), the ridges on the scales of *Acrolepis* radiate from a single ruga on the posteroventral end of the scale (Fig. 9). Unfortunately, none of the scales on specimen QMF35239 are complete as most are missing their posterior edge (Fig. 5A), and it is not possible to determine whether their ridges radiate from a single ruga. The ornamentation on the scales of *Acrolepis* appears to differ somewhat from that of type 3 (QMF35239, Fig. 9; Fig. 5A, B).

Dziewa (1977) also noted that height never exceeds length in the scales of *Acrolepis*, and although most of the type 3 scales are greater in length than depth, the lateral line scales of QMF35239 are slightly greater in height than length. Height decreases relative to length toward the dorsal, ventral, and caudal body margins of

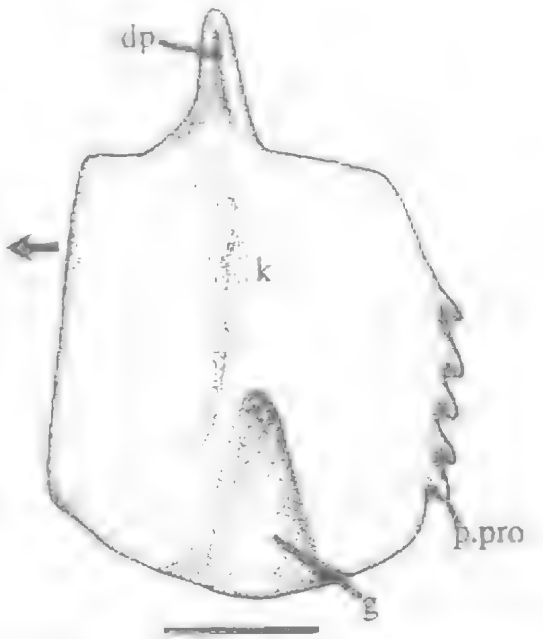



FIG. 8. Scale type 6, QMF35242, a composite reconstruction based on several incomplete anterior body scales. dp = dorsal peg, g = groove, k = keel, p.pro = posterior projections. Arrow = anterior. Scalebar = 1mm.

*Acrolepis* (Dziewa, 1977, 1980), and in these areas, the scales are shaped much like those of type 3 (pers. obs.).

Scale type 3 is also similar in shape, size and ornamentation to the body scales of members of *Brookvalia*, being rhomboid with 3-4 rugae. Most of the members of *Brookvalia* had scales with 3 or fewer oblique ridges, although the Middle Triassic *B. latipennis* had up to 4 rugae (Wade, 1935; Hutchinson, 1973). A distinct difference between the scales of type 3 and those of *Brookvalia* is that, in those of *Brookvalia*, the ornamenting ridges run obliquely from the posterodorsal to the anteroventral corners, while in the type 3 scales the ridges are oriented obliquely anterodorsal to posteroventrally. Thus, the type 3 scales bear the closest resemblance to scales of *Acrolepis* and may represent a new species given its slight variation in ornamentation from those described previously.

In size, shape, and lack of ornamentation, the type 4 scales are similar to those of the perleidids, *Pristisomus gracilis* and *Tripelta dubia*, described by Woodward (1890) from the Terrigal Formation. Based on the position of the lateral line, which crosses obliquely the uppermost

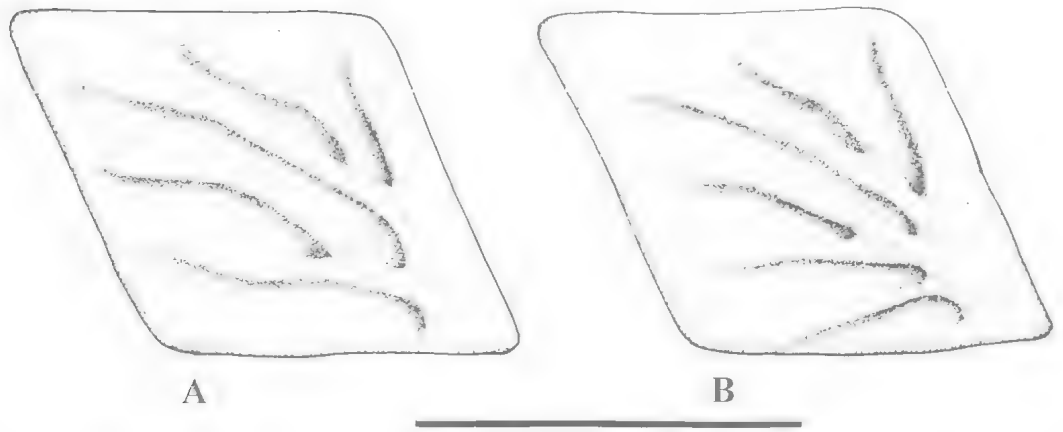



FIG. 9. Scales from the lateral line area of *Acrolepis hamiltoni* and *A. tasmanicus*, showing details of the ornamentation. Adapted from Dziewa (1977, fig. 11). A, *A. hamiltoni*, B, *A. tasmanicus*. Scalebar = 1mm.

quarter of the scale, scale type 4 is most similar to *P. gracilis*. In *T. dubia* the lateral line appears to pass through the midline of the scales (Woodward, 1890, Plate 6, fig. 4).

Turner (1982) reported the first actinopterygian, *Saurichthys* cf. *S. gigas* (Woodward, 1890), from the Arcadia Formation and suggested (pers. com. 1996) that scale type 4 might have belonged to this species. Material assigned to *Saurichthys* has been recovered from both QML78 and QML215, and includes a partial skull and a number of rostral fragments, some of which retain the lower jaws. An examination of the material led Dr A. Tintori (University of Milan) to regard it as the most primitive member of the genus (Turner, pers. com., 1996).

*Saurichthys madagascariensis* is the only saurichthyid described with a complete covering of body scales (Rieppel, 1980), this being regarded as a primitive character of *Saurichthys*. Other members of the genus have a reduced scalation consisting of 4 longitudinal rows of scales (Rieppel, 1980). The scales of *S. madagascariensis* are differentiated in shape and, with the exception of the elongated series, are ornamented characteristically with a shagreen of ganoine tubercles. The dorsal and ventral series consist of triangular scales that have a keel on the internal surface, posteriorly, which fits into a groove on the external surface at the anterior end of the succeeding scale. Immediately above the ventral series is a series of greatly elongated scales ornamented with dorsoventrally oriented ganoine ridges, rather than tubercles. Above this elongated series is a mid-lateral row of round-square shaped scales, above which was a series of slightly elongated rhomboidal scales, and two series of small rhombic scales, situated below the dorsal series of triangular scales. The type 4 scales bear no similarity to those of *S. madagascariensis* and it seems more likely that they belong to one or a number of different perleidids, similar to those described from the Terrigal Formation.

The lateral-line scales of type 5 are twice as deep as they are wide. In this sense they are similar to several of the Perleididae described by Woodward (1890) and later by Wade (1940) from the Terrigal Formation. Scales of *Chriotichthys gregarius* and *Zeuchthiscus australis* are also twice as deep as they are long; the depth of the scales of *Tripelta dubia* and *Pristisomus gracilis* is greater than double the length. Woodward (1890) noted that where the lateral line passes through the scales of *C. gregarius*, an external ridge is present. Although it is stated that the line crosses the scales near the dorsal edge, in two figured specimens the lateral line may be observed to cross the more posterior flank scales almost through the midline (Woodward, 1890, Plate 6, figs 6,7). Scale type 5 also shows a ridge along the lateral line which passes approximately through the middle of the scales. This ridge was not reported on the scales of *Z. australis* but Woodward (1890) did note that the lateral line was well marked. The scales of type 5 and those of *C. gregarius* are also similar in possessing thick unornamented scales with an extensive ganoine layer.

Scale type 6 must be the most distinctive of all the scale types recovered from the Arcadia Formation, yet none of the Early Triassic

actinopterygians have comparable scales which are figured. A number of taxa from earlier and later periods had scales similar to type 6. Traquair (1877) figured a number of Carboniferous fish with scales similar in structure to type 6, most of which were from the family Elonichthyidae. Jubb & Gardiner (1975) assigned *Oxygnathus browni* Broom (1909) from the Cynognathus Zone of South Africa to *Elonichthys*, but did not figure its scales. In the original description of the specimen Broom (1909) described its anterior body scales as thin and ornamented with 8 or 9 irregular posteroventrally directed ridges. In many cases these ridges protrude beyond the posterior border of the scales and when viewed from the ventral surface appear similar to the projections on scale type 6. Schultze (1966) described and figured the scales of several species of *Pholidophorus* that are also similar, although this taxon is generally found in sites more recent than the Early Triassic.

*Dicellopyge* is another Early Triassic genus that might have had scales similar to those of type 6. Hutchinson (1975) reported that the scales of this genus had pectinated posterior edges, as do the type 6 scales. Unfortunately, the scales of *Dicellopyge* were not figured, and I have been unable to verify their similarity.

## CONCLUSIONS

None of the scales described above are attributable to *Saurichthys* cf *S. gigas*, the only actinopterygian genus previously known from the Arcadia Formation. One of the scale types may belong to a new species of *Acrolepis* (Acrolepidae), 2 may be perleidids and 2 others are so generalised that they cannot be assigned to any of the known Triassic actinopterygians. Lastly, scale type 6, although distinctive, could not be compared with actinopterygians described as having similar scale morphology because their scales were not figured. Despite the taxonomic uncertainty, the scales provide evidence of at least 6 new taxa in the Arcadia Formation and increase the taxonomic diversity of the actinopterygian fauna from QML78 and QML215 significantly.

## ACKNOWLEDGEMENTS

I thank Anne Warren and Ross Damiani (La Trobe University) for their valued comments on drafts of this manuscript and Susan Turner (Queensland Museum) whose advice about the scales was greatly appreciated. Thanks also to the Queensland Museum for allowing me to work on the Arcadia Formation material. Photographs were taken by Russell Baader at La Trobe University. Thanks also to Ralph Molnar and Peter Jell (Queensland Museum) for refereeing the paper. This work was carried out as part of my doctoral research, financial support for which came from La Trobe University.

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# HALACARID FAUNA OF THE GREAT BARRIER REEF AND CORAL SEA: THE GENERA *AGAUOPSIS* AND *HALACAROPSIS* (ACARINA: HALACARIDAE)

JÜRGEN C. OTTO

Otto, J.C. 1999 06 30: Halacarid fauna of the Great Barrier Reef and Coral Sea: the genera *Agauopsis* and *Halacaropsis* (Acarina: Halacaridae). *Memoirs of the Queensland Museum* **43**(2): 797-817. ISSN 0079-8835.

Six new species of *Agauopsis* and one new species of *Halacaropsis* are described from the Great Barrier Reef Marine Park and adjacent Coral Sea reefs, namely *Agauopsis benziei*, *A. capillosa*, *A. decorata*, *A. fenneri*, *A. narinosa*, *A. ripa* and *Halacaropsis nereis*. The species *Agauopsis okinawensis* Bartsch is recorded for the first time from Australian waters, and *A. aequilivestita* Bartsch for the first time from the eastern part of the continent. The previously unknown males of *A. aequilivestita* and *A. okinawensis* are described and a key to Australian species of *Agauopsis* is presented. ❐ *Halacarids, Agauopsis, Halacaropsis, Great Barrier Reef, Australia.*

*Jürgen C. Otto, (email:j.otto@aims.gov.au), Australian Institute of Marine Science, PMB 3, Townsville 4810, Australia; 24 February 1999.*

Aquatic mites of the family Halacaridae are most abundant and diverse in marine habitats but also occur freshwater and range in size from 0.1-2mm. They are unable to swim and are therefore part of the benthos. More than 900 species have been described to date. Until a few years ago relatively few species were described from Australia and these were the result of sporadic collecting at just a few localities (Otto, 1994). However, recently 88 species of halacarid mites were found around the relatively small Rottnest Island (Western Australia) after only 14 days of collecting activity, which led to a dramatic increase in the number of described Australian species (Bartsch, 1992a,d; 1993a,b,c,d; 1994a,b; 1996a,b; 1997a,c; for an accurate account of all halacaroids described until 1998 see Halliday, 1998).

On the basis of such figures it appears likely that the species presently known from Australia represent only a fraction of those that inhabit the coastal waters of this continent. Further studies on Australia's extensive coast are necessary to reveal the full extent of halacarid diversity on this continent. In particular, the tropical north of the continent has barely been investigated in regard to its halacarid fauna, the only records being of 4 species of *Copidognathus* found in Darwin Harbour (Bartsch, 1997b) and 1 species of *Copidognathus* collected on the Great Barrier Reef (GBR) (Bartsch, 1996c).

The present study forms part of a project aimed at investigating the halacarid fauna of Australia's GBR, adjacent coast and Coral Sea reefs. Among the halacarids found to date are 8 species of *Agauopsis* and 1 species of the closely-related genus *Halacaropsis*. Seven of these are new to science and are described herein.

## METHODS

Sand, coral rubble and algae, all substrates in which halacarids are known to occur, were collected by hand either intertidally or from various depths usually using SCUBA. A single sample from 51m depth was taken by a mechanical grabbing device. Mites were extracted by washing the substrates in a bowl of water and decanting the supernatant through a 100µm sieve. All material was collected by the author except where stated otherwise. Mites were cleared in lactic acid and mounted in PVA (Boudreaux & Dosse, 1963). Drawings were made with the aid of a camera lucida.

In the accounts of each species only one sex is described in detail, while for the opposite sex only characters that differ are described. Measurements are in micrometres (µm). Terminology follows Bartsch (1993e) and includes: areolae – areas on dorsal and ventral plates with cuticular structure differing from remainder of plates; costae – longitudinal areolae on PD and AD; parambulacral setae – small setae at tip of tarsus; cornea – refractile body visible on the ocular plate in deeper cuticular layers. Abbreviations: AD, anterodorsal plate; AE, anterior epimeral plate; GA, genitoanal plate; GO, genital opening; OC, ocular plate; PD, posterodorsal plate; PE, posterior epimeral plate; P-2, P-3, P-4, 2nd, 3rd and 4th palp segments (starting from base); I-IV,

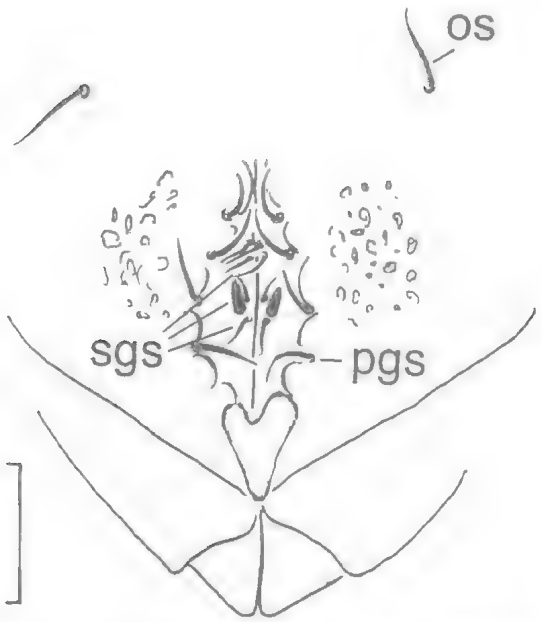



FIG. 1. *Agauopsis aequilivestita* Bartsch, male genital opening. Scale line = 25μm.

leg I to leg IV; ar, areola; co, costa; pas, single parambulacral setae; double-pas, doubled parambulacral setae; os, outlying setae; pgs, perigenital setae; sgs, subgenital setae. All material is deposited in the Queensland Museum (QM), at the Museum of Tropical Queensland branch in Townsville (MTQ), unless stated otherwise. Abbreviations for other depositories: ANIC, Australian National Insect Collection (Canberra, Australia); UQIC, University of Queensland Insect Collection (Brisbane, Australia); ZMH, Zoologisches Museum Hamburg (Hamburg, Germany).

## SYSTEMATICS

### **Agauopsis** Viets

*Agauopsis* Viets, 1927: 94; 1956: 687. Newell, 1947: 21, 38, 184; 1971: 28; 1984: 215. Bartsch, 1986: 165; 1993e: 57; 1996a: 2; Otto, 1994: 35.

TYPE SPECIES. *Agaue brevipalpus* Trouessart, 1889b, by original designation.

DIAGNOSIS. Body heavily armoured; setae on dorsal striated integument not distinctly longer than setae on dorsal plates. Anterior epimeral plate entire, with 3 pairs of setae. Leg I heavier than legs II-IV, with heavy spiniform setae on telofemur, genu, tibia and tarsus. Spine on tarsus I in medial position, much shorter than tarsus. Tarsi straight, not curved. Median claws absent or inconspicuous. Tarsi III and IVusually lacking ventral setae (parambulacral setae excluded).

### **Agauopsis aequilivestita** Bartsch
(Fig. 1)

*Agauopsis aequilivestita* Bartsch, 1996a: 2.

MATERIAL. Great Barrier Reef Marine Park; QMS105141, F, and ZMH, F, 19.20.12°S 149.02.85°E, Elizabeth Reef, 25. Dec. 1997, coarse sand at 3m; QMS105142-105144 3F, 18.25.93°S 147.21.11°E, Faraday Reef, 13 Apr. 1998, coarse sand & rubble at 10m, sand at 2m, and coarse sand & rubble at 2m, respectively; QMS105145, F, 18.41.91°S 147.06.49°E, Loadstone Reef, 12 Apr. 1998, sand & rubble at 2m; QMS105146, F, Carter Reef, ca. 14.32°S 145.35°E, 11 Oct. 1998, coarse sand at 0.5m. Coral Sea: QMS105147-105153, 7F, ANIC, F, ZMH, F; QMS105154-105159, 6F, Lihou Reef, ca. 17.25°S 151.40°E, 20-22 July 1998, D. Fenner, sand at 5-7m; QMS105160, F, Willis Islet, ca. 16.18°S 149.58°E, 15 Sept. 1998, G.A. Diaz-Pulido, coral rubble (fine), 0-10m.

REMARKS. The above listed specimens are the first records of this species from the Australian east coast. The species was known previously only from Rottnest I. in SW Australia. It is closely related to *Agauopsis punctatus* Bartsch, 1981, from the Moçambique channel.

Bartsch (1996a) described an oblong area lacking rosette pores on the posterodorsal plate of *A. aequilivestita*. Such an oblong area is absent in all specimens from the Coral Sea reefs but present, although variable in size and sometimes barely visible, in all specimens collected on the GBR. These differences could indicate that Coral Sea and GBR populations are reproductively isolated and as a result may have diverged over time. The reefs of the Coral Sea are separated from the GBR by a >1,000m deep trench which may constitute a significant barrier for halacarids that lack planktonic life stages.

The present material contains previously unknown males which differ from the female as follows: Idiosoma 372-400 long. 8-14 pgs surrounding GO, inserted between cuticular callocities (Fig. 1); pair of outlying setae inserted anterolateral to GO. GO with 5 pairs sgs, 2 pairs anterior and 3 pairs posterior, the middle pair of the posterior group much heavier than the others. Cuticle surrounding GO with irregular shaped pits.

**Agauopsis benziei** sp. nov.
(Figs 2, 3)

ETYMOLOGY. In honour of Dr John Benzie who has given his continuous support for the present project.

MATERIAL. HOLOTYPE: QMS105161, F, Great Barrier Reef Marine Park, Elizabeth Reef, 19°20.12'S 149°02.85'E, 25 Dec. 1997, coarse sand at 3m. PARATYPES: Great Barrier Reef Marine Park: QMS105162, F, ZMH, F, Elizabeth Reef 19°20.12S 149°02.85E, 25 Dec. 1997, coarse sand and rubble at 3m; QMS105164, F, Bramble Reef, 18°25.25'S 146°40.65'E, 10 Apr. 1998, medium coarse sand at 3-6m; QMS105163, F, Bramble Reef, 18°25.25'S 146°40.65'E, 10 Apr. 1998, chunks of coral rubble at 3-6m; ANIC, F, Loadstone Reef, 18°42.03'S 147°06.54'E, 12 Apr. 1998, coarse sand & rubble at 12-15m; QMS105165-105166, 2F, Pandora Reef, 18°49'S 146°26'E, 22 Jan. 1997, coarse sand at 1m; QMS105175, F, QMS105167 M, between Myrmidon Reef and Faraday Reef, 18°23.64'S 147°20.42'E, 13 Apr. 1998, fine-medium coarse sand, at 51m; QMS105169, M, Rosser Reef, ca. 15°37'S 145°33'E, 8 Oct. 1998, sand at 2m; QMS105174, F, No Name Reef, ca. 14°39'S 145°40'E, 9 Oct. 1998, chunky coral rubble & sand at 9m; QMS105170, F, Yonge Reef, ca. 14°36'S 145°38'E, 20 Sept. 1998, G. Díaz, medium coarse sand at 7m. Coral Sea: QMS105171, M, Lihou Reef NW, ca. 17°25'S 151°40'E, 22 July 1998, D. Fenner, sand at 8m; QMS105168, M, South Willis Islet, ca. 16°18'S 149°58'E, 15 Sept. 1998, G.A. Diaz-Pulido coll., coral rubble (fine), 0-10m; QMS105173, F, QMS105172, M, Chilcott Islet, 16°56.51'S 150°0.4'E, 14 Sept. 1998, G.A. Diaz-Pulido coll., coarse sand, 1-14m.

*Female*. Idiosoma 412-470 long (holotype 443). AD and PD closely associated (Fig. 2A); no setae in membranous cuticle between them. Frontal spine stout, roughened and medially notched. AD posteriorly narrowing, truncate; areola shaped as in Fig. 2A, marked by double row of deep pits and numerous fine canaliculi in deeper cuticular layers; transverse part of areola set off sharply from anterior part of plate; part of plate circumscribed by areola with thick cuticular bars forming conspicuous reticulate ornamentation, floor of each polygon roughened by shallow pits; rest of plate papillate; with a pair of setae inserted directly anterior to areola. OC with 2 corneae and transverse areola (marked by pits and in deeper cuticular layers by numerous canaliculi) on elevated part of plate; posterior to corneae with pore, anteriorly with a seta; anterior and posterior parts pf plate papillate. PD with pair of prominently elevated costae, marked by double row of deep pits and in deeper cuticular layers by numerous canaliculi; costa over most of its length 2 pits wide, posteriorly swollen and about 3-4 pits wide; remainder of plate conspicuously reticulated; 2 pairs of setae near anterolateral margin of plate, 3rd pair of setae approximately half way along plate. Pair of adanal setae inserted dorsally on reticulated anal cone. AE with very faint reticulate ornamentation; pierced by canaliculi, those directly posterior to the anterior and posterior pairs of epimeral setae and posterior to the pair of epimeral pores slightly coarser than canaliculi on rest of plate; posterior margin with series of pore-like structures (Fig. 2B). PE dorsally with 3 pitted areolae, lateral to dorsal seta, just posterior to dorsal seta and anterior to insertion of leg IV, respectively (Fig. 2A); ventrally with 3-4 areolae, of which the posterior one is marked by relatively deep pits while the others are marked by fine canaliculi. GA punctate and very faintly reticulate; few pore-like markings in anterior half of plate along lateral margins (Fig. 2B); anterolateral to GO with pitted areolae; cuticle posterolateral to GO thickened and roughened; position of 3 pairs of pgs as in Fig. 2B, anterior pair well removed from anterior end of GO.

Ventral gnathosomal base with conspicuous lateral protrusion (Fig. 2D); distinctly pitted throughout, most conspicuously on protrusion; pair of setae separated by <1/5th of width of gnathosomal base. Dorsal gnathosomal base roughened. Rostrum longer than gnathosomal base; rostral sulcus extending along 2/3rd of rostrum. Medial spine on P-3 slender and tapering; P-4 with 2 slender setae inserted half way along segment, one shorter than the other.

Telofemora and tibiae of legs with reticulate ornamentation, most conspicuous on medial flanks (indicated for leg I in Fig. 3A). Telofemur I with a sharp ventral ridge carrying a proximal protuberance, dorsally with a series of conspicuous pits. Chaetotaxy (trochanter-tibia): I 1-2-9(10)-5-11 (Fig. 3A); II 1-2-7-4-8 (Fig. 3B); III 1-2-4-3-6 (Fig. 3C); IV 1-2-4-3-6 (Fig. 3D). Leg I with the following complement of heavy spiniform setae: 1 ventral and 3 medial on telofemur, 1 medial on genu, 3 medial and 2 ventral on tibia, 1 medial on tarsus; 2 of the 3 medial spiniform setae on tibia closely associated (Fig. 3A). Tibia II with 3 spiniform apically denticulate setae, the 2 distal ones longer than the proximal one (Fig. 3B). Tibiae III and IV with 2 such setae, proximal one much shorter than distal one (Fig. 3C,D). Tarsus I with pair of pas, pair of double-pas, and 1 ventral seta. Tarsus II with pair of double-pas, ventral member spur-like. Tarsi III and IV with 1 ventral seta and pair of pas, the lateral pas spur-like. Paired claws on tarsus I

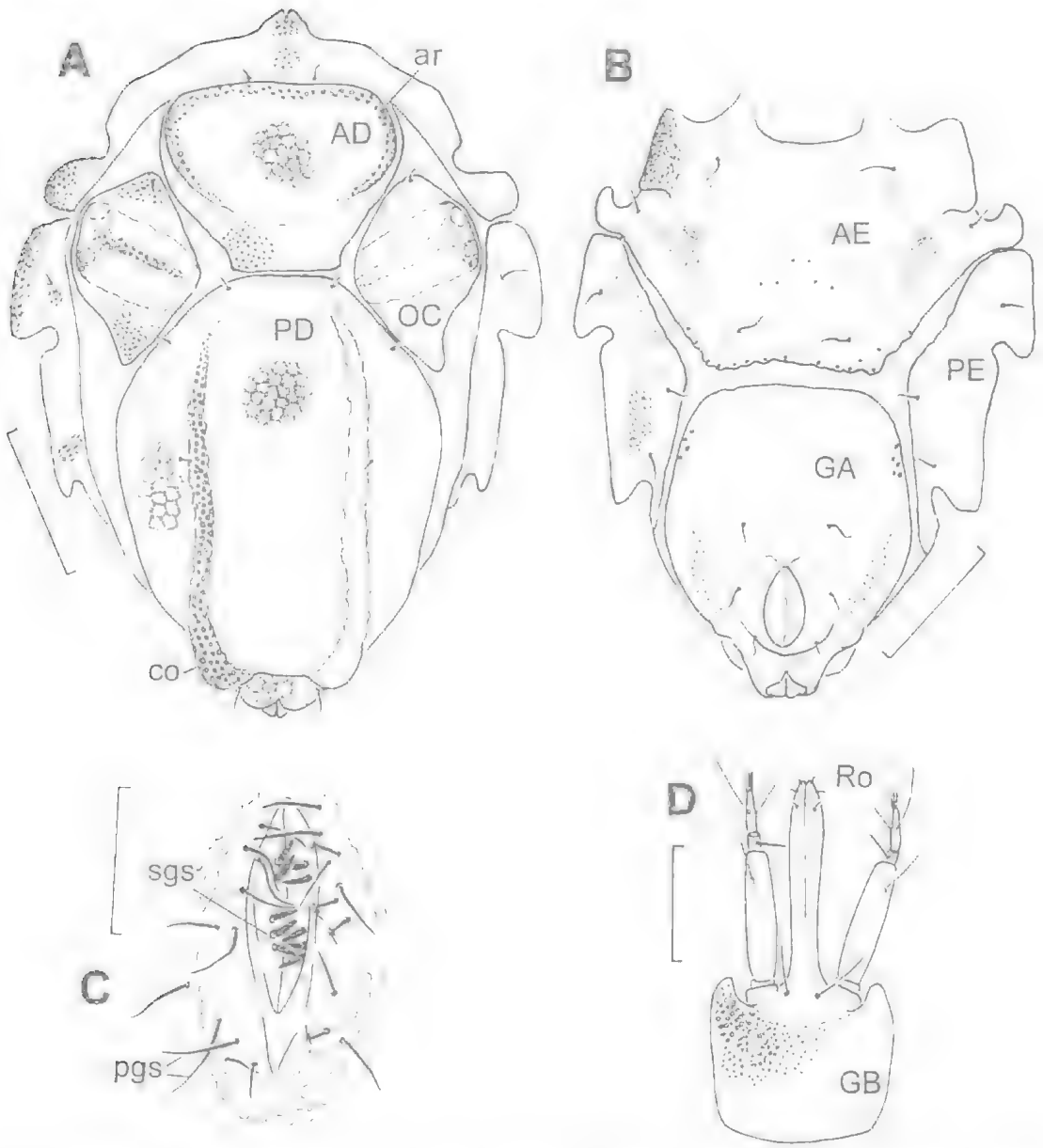



FIG. 2. *Agauopsis benziei* sp. nov., adult: A, dorsal idiosoma of female; B, ventral idiosoma of female; C, genital opening of male; D, ventral gnathosoma. Scale lines: A,B = 100µm; C = 25µm; D = 50µm

smooth, those of other legs with accessory process and pecten. All tarsi with median claw.

*Male*. Idiosoma 399-448 long. GO surrounded by ca. 22-24 pgs (Fig. 2C); genital valve with 5 pairs of sgs, 2 pairs anteriorly and 3 pairs posteriorly.

REMARKS. *Agauopsis benziei* sp. nov. differs from all its congeners by the shape of the areola on the anterodorsal plate. In *A. benziei* it is a narrow band in the shape of an inverted bowl. *A. benziei* is a typical representative of the *conjuncta* group (see Bartsch, 1986) which is characterised by the costae on the posterodorsal plate carrying relatively deep pits, the anterodorsal plate narrowing posteriorly and tibia I possessing five spines. The other species in this group are *A. bathyalis* Bartsch, 1989, *A.*

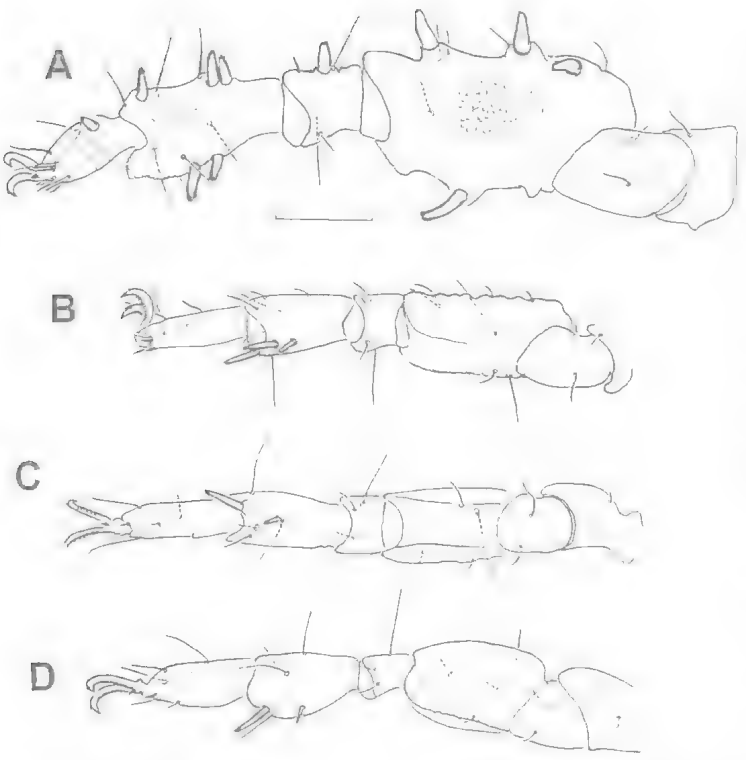



FIG. 3. *Agauopsis benziei* sp. nov., adult: A, leg I, ventromedial; B, leg II, ventromedial; C, leg III, ventral; D, leg IV, lateral. Scale lines = 50μm.

*conjuncta* Viets, 1940, *A. meteoris* Bartsch, 1973, and *A. minor* (Trouessart, 1894).

**Agauopsis capillosa** sp. nov.
(Figs 4,5)

ETYMOLOGY. Latin, *capillosa* = hairy; referring to the numerous fine filaments on the leg setae.

MATERIAL. HOLOTYPE: QMS105176, F, Great Barrier Reef Marine Park, Phillips Reef, 18°58.49'S 146°36.94'E, 16 Apr. 1998, muddy rubble at 12m. PARATYPE: QMS105177, F, Great Barrier Reef Marine Park, Elizabeth Reef, 19°20.12'S 149°02.85'E, 25 Dec. 1997, coral rubble at 10m.

*Female*. Idiosoma in holotype and paratype 410 long. Membranous cuticle with 1 pair of setae near posterolateral margin of AD (Fig. 4C). AD with prominent frontal spine ornamented with few slightly raised panels; lateral to frontal spine with pair of protuberances; lateral part of plate with pair of areolae consisting of a single row of quadrangular panels, each panel associated with an alveolus in deeper cuticular layers; panels roughened by minute tubercles, not pierced by canaliculi; between areolae with reticulate ornamention formed by cuticular bars surrounding pitted polygons. OC acuminate posteriorly, punctate and faintly reticulate; with 2 corneae and posterior to these with a pore; transverse areola inconspicuous, only represented by a few solid panels. PD with reticulate ornamentation similar to that on AD; pair of narrow raised costae (consisting of a single row of quadrangular panels overlying alveoli) strongly converging posteriorly; 3 pairs of setae as illustrated (Fig. 4C); posteriorly with pair of pores. AE not extending beyond insertion of legs III; posterior margin slightly concave (Fig. 4A); punctate and with inconspicuous reticulate ornamentation throughout; posterior to insertions of legs I and II with papillate areolae; half way along plate on either side with group of several scars continuing underneath surface as sickle-shaped sclerites. PE punctate, laterally with papillate areolae. GA punctate; 3 pairs of pgs, the anteriormost pair heavier than the others; lateral to GO with papillate areolae.

Ventral gnathosomal base swollen posterolaterally; punctate; laterally with reticulate ornamentation (Fig. 4B); pair of setae inserted at distance <1/3rd of width of gnathosomal base. Rostrum longer than gnathosomal base. Palp longer than rostrum; P-3 with slender and tapering spine which is at least twice as long as P-3; P-4 subequal in length to P-2, with 2 fine tapering setae and 2 shorter blunt setae apically.

Chaetotaxy of legs (trochanter-tibia): I 1-2-8-5-8 (Fig. 5A), II 1-2-5-4-5 (Fig. 5B), III 1-2-3-3-4 (Fig. 5C), IV 0-2-3-3-4 (Fig. 5D), all setae, except those that are spiniform, with numerous fine filaments (Fig. 5). Leg I (Fig. 5A) with the following arrangement of heavy spiniform setae: 2 ventral and 3 medial on telofemur, 1 medial and 1 much smaller ventral on genu, 1 ventral and 2 medial on tibia, 1 medial on tarsus, each spiniform seta with denticles apically, some of which are arranged in distinct rows. Setae of legs III and IV longer than those of

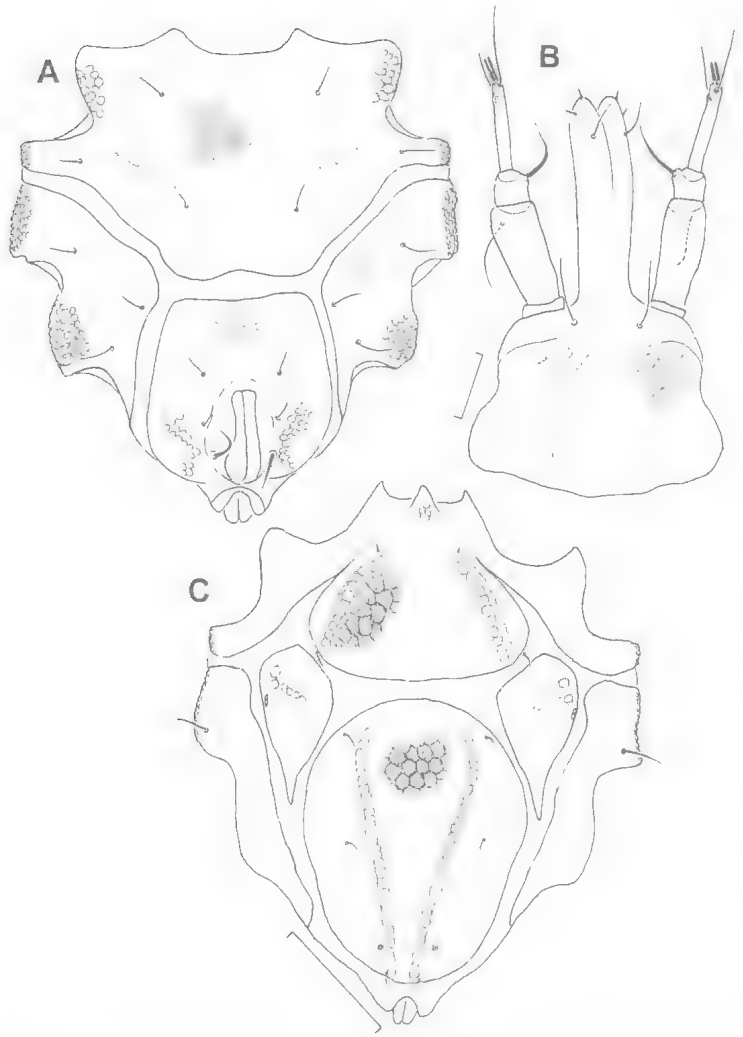



FIG. 4. *Agauopsis capillosa* sp. nov., adult: A, dorsal idiosoma of female; B, ventral idiosoma of female; C, ventral gnathosoma. Scale lines: A, B = 100μm; C = 25μm.

legs I and II. Tarsus I with pair of pas and pair of ventral setae; tarsus II with 1 pas laterally, without ventral setae; tarsi III and IV without pas or ventral setae. All tarsi with pair of smooth paired claws, those of leg I smaller than those of legs II-IV; median claw on tarsus I present, on other tarsi absent.

*Male*. Unknown.

REMARKS. In *Agauopsis capillosa* the apical palp segment is at least as long as palp segment P-2, which is known otherwise only for *A. okinavensis* Bartsch, 1986. *A. capillosa* differs from *A. okinavensis* in that the anterior epimeral plate is not extending beyond the level at which legs III are inserted.

*A. capillosa* is most similar to *A. okinavensis*, previously the only known member of the *okinavensis* group (see Bartsch, 1986). Both species share a number of otherwise unusual characters on the basis of which *A. capillosa* is here assigned to the *okinavensis* group. These characters, which may be used to define this species group are: papillate areolae on anterior and posterior epimeral plates; narrow costae with quadrangular panels that are not pierced by canaliculi; projections lateral to the frontal spine; a very long palp tarsus with 2 filiform setae apically; a spine on palp segment P-3 that is at least twice as long as the segment; smooth claws on all tarsi and relatively long leg setae, in particular on legs III and IV.

Bartsch (1986) regarded the posteriorly extended anterior epimeral plate of *A. okinavensis* as a character by which the *okinavensis* group should be defined. However, the absence of this character in *A. capillosa* indicates that the extended plate is not a common character of species in this group.

Bartsch (1986) was uncertain whether or not to include *A. pteropes* Bartsch, 1986, in the *okinavensis* group and postponed the decision until further material was collected. I do not regard *A. pteropes* as a species of the *okinavensis* group since it lacks all of the aforementioned characters.

**Agauopsis decorata** sp. nov.
(Fig. 6)

ETYMOLOGY. Latin, *decorata* = adorned; referring to the garland-like ornamention of the anterior epimeral plate.

MATERIAL. HOLOTYPE: QMS105178, F, Great Barrier Reef Marine Park, Elizabeth Reef, 19°20.12'S

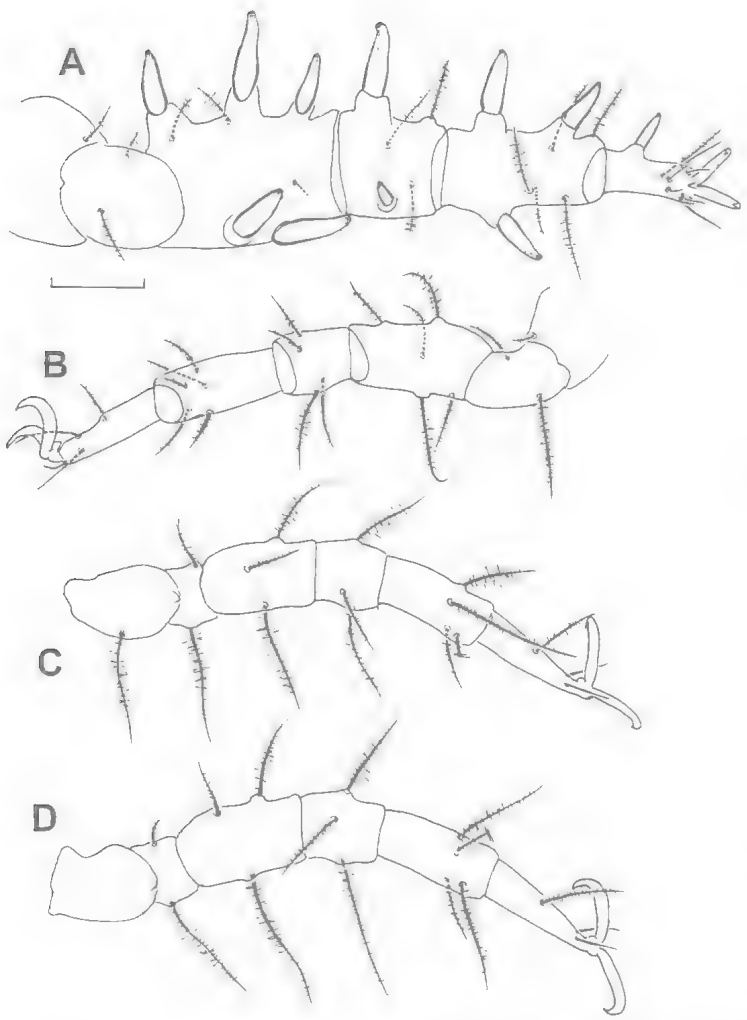



FIG. 5. *Agauopsis capillosa* sp. nov., adult: A, leg I, ventral; B, leg II; C, leg III, dorsal; D, leg IV, dorsal. Scale lines = 50μm.

149°02.85'E, 25 Dec. 1997, coral rubble at 10m. PARATYPES: Great Barrier Reef Marine Park: QMS-105179, F, data as for holotype; QMS105180-105181, 2F, data as for holotype except: 24 Dec. 1997, coral rubble at 16-26m; QMS105187, F, Fantome I., 18°42.14'S 146°30.48'E, 6 Apr. 1998, coral rubble covered with mud; QMS105182, F, Fantome I., 18°42.11'S 146°31.51'E, 15 Apr. 1998, chunks of coral rubble at 2m; ANIC, F, Pandora Reef, 18°48.92'S 146°25.76'E, 22 Jan. 1998, chunks of coral rubble with rich epifauna/-flora, 0.5m; ZMH, F, Loadstone Reef, 18°42.03'S 147°06.54'E, 12 Apr. 1998, coral rubble at 12-15m; QMS105183, F, Townsville, Magnetic I., 16 Nov. 1996, sand at 2-6m; QMS105184, F, Bramble Reef, 18°25.25'S 146°40.65'E, 10 Apr. 1998, chunks of coral rubble at 3-6m; QMS105185, F, between Myrmidon and Faraday Reefs, 18°23.64'S 147°20.03'E, 13 Apr. 1998, fine-medium coarse sand at 51m; QMS105186, F, No Name Reef, ca. 14°39'S 145°40'E, 9 Oct. 1998, chunky coral rubble and sand at 9m.

*Female.* Idiosoma 368-396 long (holotype 375). Outline as in Fig. 6A,B. Membranous cuticle between plates with only 1 pair of setae, situated on small platelets (Fig. 6A). AD with prominent pointed frontal spine; posterior to spine with slightly raised areola pierced by groups of canaliculi; laterally with pair of sharp dorsolaterally directed ridges, at their anterior end with pair of setae; along the inside of ridges with single row of rosettes of ca. 6-8 canaliculi, underneath each rosette in deeper cuticular layers an alveolus; part between ridges strongly elevated over lateral portions of plate, with cuticular bars forming reticulate ornamentation pattern, cuticle within each polygon pitted; posterior margin of plate almost straight. OC with 2 corneae, posterior to these an inconspicuous pore; transverse areola consisting of few canaliculi rosettes overlying an alveolus; areola and corneae on elevated part of plate; posterior part of plate with papillae forming an inconspicuous reticulate pattern. PD fused with anal cone; with pair of narrow, slightly raised costae consisting of single (in short sections doubled) row of canaliculi rosettes, underneath each rosette an alveolus; area between costae with conspicuous reticulate ornamentation, lateral to costae with papillae arranged in polygons and forming a less conspicuous reticulated pattern; anterior to anal cone with a transverse thickened areola, pierced by canaliculi rosettes and well separated from costae; with 1 pair of setae at anterolateral margin of PD, another pair approximately half way along PD, and a 3rd pair on anal cone. AE very faintly reticulate, over most parts with scattered canaliculi; rosettes of ca. 13-17 conspicuous canaliculi arranged to

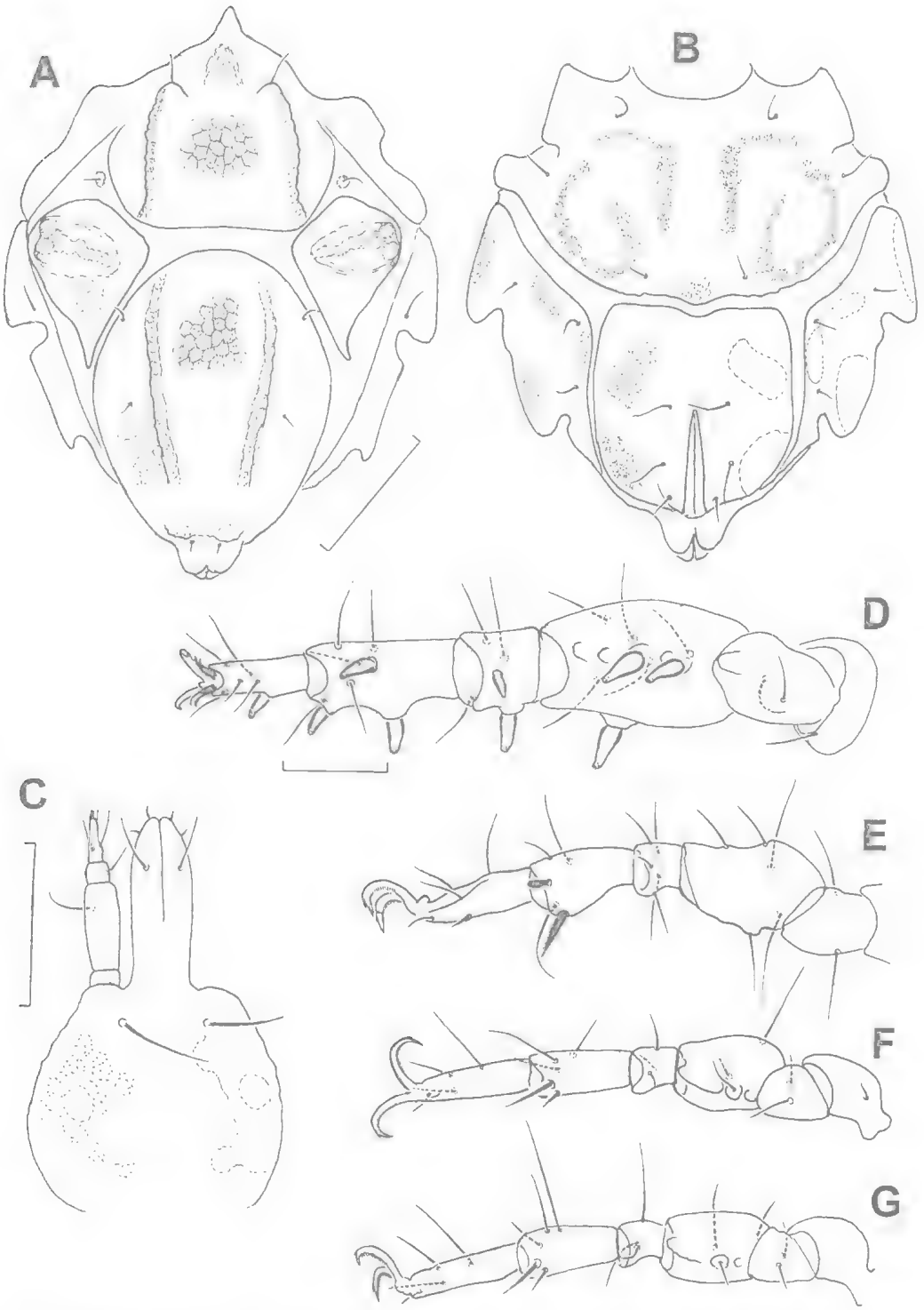



FIG. 6. *Agauopsis decorata* sp. nov., adult; A, dorsal idiosoma of female; B, ventral idiosoma of female; C, ventral gnathosoma; D, leg I, ventral; E, leg II, medial; F, leg III, ventrolateral; G, leg IV, ventrolateral. Scale lines: A, B = 100μm; C-G = 50μm.

form garland-like ornamentation pattern which is interrupted just posterolaterally of anterior pair of epimeral setae (Fig. 6B); posterior margin medially with bulged area containing an areola consisting of several canaliculi rosettes. PE ventrally with at least 4 areolae consisting of canaliculi rosettes. GA slightly indented anteriorly; 3 pairs of pgs positioned as in Fig. 6B, anteriormost pair level with anterior margin of GO; anterolaterally and posterolaterally with areola consisting of canaliculi groups and faint polygonal panels.

Ventral gnathosomal base laterally with pair of areolae consisting of few inconspicuous polygonal panels with canaliculi; circular scar on either side without canaliculi (Fig. 6C); between areolae pitted; anteriorly with pair of setae separated by <1/2 the width of gnathosomal base. Rostrum shorter than gnathosomal base. Palp with slender and tapering spine on P-3; P-4 with 2 setae in proximal half, both of subequal length.

Legs chaetotaxy (trochanters-tibia): I 1-2-8-5-8 (Fig. 6D), II 1-2-5-5-5 (Fig. 6E), III 1-2-3-3-5 (Fig. 6F), IV 0-2-3-3-5 (Fig. 6G). Leg I with the following set of heavy spiniform setae: 2 ventral and 1 anterior on basifemur, 1 ventral and 1 longer medial on genu, 1 ventral and 2 medial on tibia, 1 medial on tarsus, all with minute denticles at tip; basifemur I with distinct ventral protuberance (Fig. 6D). Tibiae II-IV with 1 ventral filiform seta on a protuberance, on tibiae III and IV flanked distally by a lamella and proximally by a second smaller protuberance; with pair of bipectinate setae, the shorter medial one clavate, the longer ventral one pointed. Tibiae III and IV with pair of slightly thickened and slightly denticulate setae, the lateral one longer than the medial one. Tarsus I with pair of double-pas and 2 ventral setae; tarsus II with 1 ventral seta and 1 lateral pas; tarsi III and IV with 1 medial pas. Paired claws on tarsus I smooth, without pecten or accessory process; claws of tarsi II-IV with pecten (more conspicuous on tarsus II than on tarsi III and IV) and inconspicuous accessory process. Median claw on tarsus I present, on II-IV absent.

*Male*. Unknown.

REMARKS. *Agauopsis decorata* sp. nov. belongs to the *ornata* group (see Bartsch, 1986, 1996a), which is common in tropical and subtropical waters but apparently absent in cooler regions (Bartsch, 1996a). Species of this group are recognisable by their garland-like ornamentation pattern on the anterior epimeral plate. Other members of this group are *A. bacescui* Konnerth-Ionescu, 1977, *A. bermudensis* Bartsch and Iliffe, 1985, *A. inflatus* Newell, 1984, *A. ornata* (Lohmann, 1893), *A. pseudoornata* Bartsch, 1985, and *A. ornatella* Bartsch, 1996a.

*A. decorata* differs from *A. bacescui* by having three instead of four spiniform setae on telofemur I, from *A. inflatus* by having a relatively shorter rostrum, from *A. bermudensis*, *A. ornata* and *A. pseudoornata* by having much narrower areolae and costae on AD and PD respectively, and from *A. ornatella* by having a raised areola posterior to the frontal spine.

**Agauopsis fenneri** sp. nov.
(Figs 7,8)

ETYMOLOGY. In honour of Dr Doug Fenner, who collected the holotype.

MATERIAL. HOLOTYPE: QMS105188, F, Coral Sea, Lihou Reef NW, ca. 17°25'S 151°40'E, 22 July 1998, D. Fenner, sand at 8m. PARATYPES: Great Barrier Reef Marine Park: QMS105190, F, ANIC, F, ZMH, F, Lizard I., Coconut Beach, 13 Oct. 1998, medium coarse sand at 0.5m; QMS105189, M, QMS105191, F, Lizard I., Coconut Beach, 13 Oct. 1998, medium coarse sand at mid tide level, sediment depth 10cm.

*Female*. Idiosoma 327-341 long (holotype 333). Outline as in Fig. 7A,C. Membranous cuticle between plates with only 1 pair of setae, situated on small platelets anterior to OC (Fig. 7A). AD with prominent pointed frontal spine; posterolateral to spine with pair of conspicuous oblong roughened swellings which are pierced by few canaliculi; posterior to swellings with pair of sharp laterally directed ridges that carry at their anterior end a pair of setae; along the inside of ridges with single row of canaliculi rosettes, each overlying an alveolus; part between ridges strongly elevated over lateral parts of plate, with cuticular bars forming reticulate ornamentation pattern, cuticle within each polygon pitted; posterior margin of plate almost straight. OC with 2 corneae and small areola consisting of few canaliculi rosettes on elevated part of plate. PD fused with anal cone; pair of narrow costae consisting of double row of canaliculi rosettes each overlying an alveolus; area between costae elevated over remainder of plate, with cuticular bars forming conspicuous reticulate ornamentation similar to that of AD; just anterior to anal cone with transverse thickened areola, pierced by canaliculi rosettes, not distinctly separated from costae; 1 pair of setae at anterolateral margin of PD, another pair

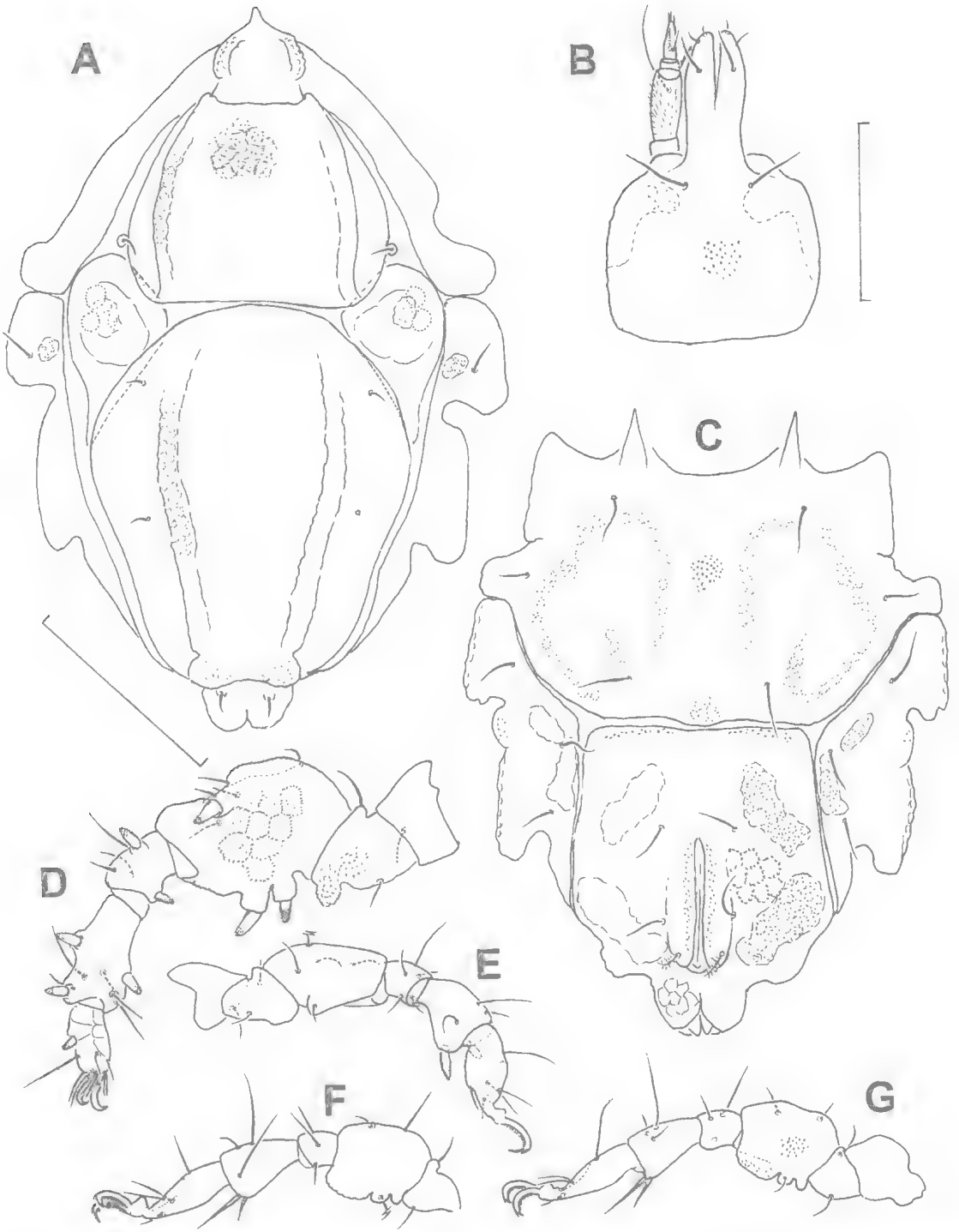



FIG. 7. *Agauopsis fenneri* sp. nov., female: A, idiosoma, dorsal; B, gnathosoma, ventral; C, idiosoma, ventral; D, leg I, ventromedial; E, leg II, lateral; F, leg III, lateral; G, leg IV, lateral. Scale lines: A = 100μm; B = 50μm; C-G = 100μm.

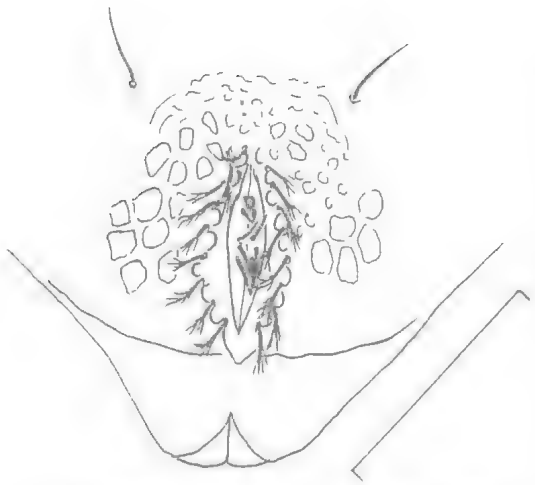


FIG. 8. *Agauopsis fenneri* sp. nov., genital opening of male. Scale line = 50μm.

approximately half way along PD, and a 3rd pair on anal cone. AE with canaliculi rosettes arranged to form garland-like ornamentation pattern; remainder of plate covered by shallow pits; posterior margin with a bulged area containing a single areola. PE ventrally with 2 areolae and dorsally with 1 areola close to dorsal seta. GA anteriorly with minute denticles; lateral to GO with 2 pairs of areolae consisting of canaliculi groups and faint polygonal panels; the the posteriormost pair of the 3 pairs of pgs covered with fine filaments; genital valves with a series of pits.

Ventral gnathosomal base pitted, lateral areolae pierced by canaliculi; anteriorly with pair of setae. Rostrum shorter than gnathosomal base. Palp segment P-2 with a cover of fine filaments. P-3 with well developed blunt and apically denticulate spine. P-4 with 2 equally long seta in proximal half.

Basifemur of leg I with distinct ventral protuberance. Telofemur I with distinct reticulation on both flanks; telofemora II-IV with reticulation only on medial flanks. Chaetotaxy (trochanters-tibia): I 1-2-8-5-8 (Fig. 7D), II 1-2-5-5-5 (Fig. 7E), III 1-2-3-3-5 (Fig. 7F), IV 0-2-3-3-5 (Fig. 7G). Leg I with the following set of heavy spiniform setae: 2 ventral and 1 anterior on basifemur (ventral ones on conspicuous protuberances), 1 short ventral and 1 longer medial on genu, 1 ventral and 2 medial on tibia, 1 medial on tarsus, all with minute denticles at tip. Tibiae II-IV with 1 ventral seta on protuberance, on tibiae III and IV flanked distally by a lamella and proximally by a second protuberance. Tibia I with a heavy ventral denticulate seta and a wide but short bipectinate ventromedial seta; tibiae III and IV with pair of tapering spiniform setae. Tarsus I with 2 ventral setae and pair of double-pas. Tarsi II-IV without ventral setae, but with 1 lateral pas. Paired claws of tarsus I smooth, those of tarsi II-IV with pecten. Median claw on tarsus I present, on tarsi II-IV absent.

*Male*. Idiosoma 313-323 long. GO surrounded by ca. 16-18 apically branched pgs, inserted between callocities (Fig. 8). Five pairs of sgs, the posterior 3 pairs longer than the 2 anterior pairs.

REMARKS. *Agauopsis fenneri* sp. nov. belongs to the *ornata* group (see Bartsch, 1986, 1996a; remarks to *A. decorata*). Within this group the only other species that possesses a pair of oblong swellings posterolateral to the frontal spine is *A. ornatella* Bartsch 1996a. *Agauopsis fenneri* differs from *A. ornatella* in that the costae on the PD are 2 canaliculi rosettes wide and only 1 areola is present at the posterior margin of the AE (versus 2 areolae in *A. ornatella*).

**Agauopsis narinosa** sp. nov.
(Figs 9,10)

ETYMOLOGY. Latin, *narinosa* = broadnosed; referring to the truncated frontal spine.

MATERIAL. HOLOTYPE: QMS105192, M, Great Barrier Reef Marine Park, Townsville, 16 Feb. 1997, algae on intertidal rocks. PARATYPES: Great Barrier Reef Marine Park: QMS105193, M, data as for holotype; ZMH, F, Cape Ferguson (S of Townsville), 19°16.09'S 147°03.05'E, 13 July 1997, algae on intertidal rocks.

*Male*. Idiosoma 340-350 long (holotype 340). Outline as in Fig. 9A,D. Membranous cuticle greatly reduced, without setae (Fig. 9A). AD with broad blunt frontal spine; posterior margin of plate convex; H-shaped raised areola ornamented with canaliculi groups, underneath each group an inconspicuous alveolus; areola 2 alveoli wide; posterior to transverse part of areola with reticulate ornamention formed by cuticular bars surrounding coarsely pitted polygons; pair of setae inserted anteriorly; at anterior ends of areola with pair of inconspicuous pores. OC with 2 corneae; transverse areola 1-2 alveoli wide. Posterior to corneae with few canaliculi, pore not seen; corneae and areola elevated over remainder of plate; anterior to areola slightly roughened, posterior to areola with faint reticulated ornamentation. PD reticulated; with pair of prominent costae (Fig. 9A) carrying canaliculi groups and alveoli in deeper cuticular layers, costa 1-2 alveoli wide; 2 pairs of setae at

anterolateral margin; 3rd pair of setae at posterior margin. AE finely punctate, posterior margin slightly undulate (Fig. 9D). PE finely punctate, with areola posteriorly. GA finely punctate, lateral to GO with areola; cuticle around GO swollen. GO surrounded by ca. 12 pgs and pair of outlying setae arranged as illustrated (Fig. 9D).

Ventral gnathosomal base laterally punctate, along median axis smooth; pair of setae separated by <1/2 the width of gnathosomal base (Fig. 9B). Rostrum subequal in length to gnathosomal base. Palp segment P-3 with slender tapering spine; one of the 2 basal setae on P-4 only 1/5 the length of the other.

Medial flanks of telofemur and tibia of leg I reticulated; telofemur I ventrally with conspicuous proximal protuberance. Tibia I apically with spine-like ventral lamella. Chaetotaxy (trochanter-tibiae): I 1-2-8-5-10 (Fig. 10A), II 1-2-6-5-6-5 (Fig. 10B); III 1-2-3-2-5-4 (Fig. 10C), IV 0-2-3-2-5-4 (Fig. 10D); Leg I with the following complement of heavy spiniform setae: 1 ventral and 2 medial on telofemur, 1 medial on genu I, 3 medial (2 of these closely associated) and 1 ventral on tibia, 1 medial on tarsus, all spiniform setae with small denticles apically; 2 spiniform denticulate setae ventrally on tibiae II-IV (Fig. 10B-D); 1 bipectinate seta medially on tibia II (Fig. 10B). The apical pair of the 3 dorsal fossary setae on tarsi III and IV branched (Fig. 10C,D). Paired claw of tarsus I with accessory process but no pecten, paired claws of tarsi II-IV with pecten and accessory process. All tarsi with median claw.

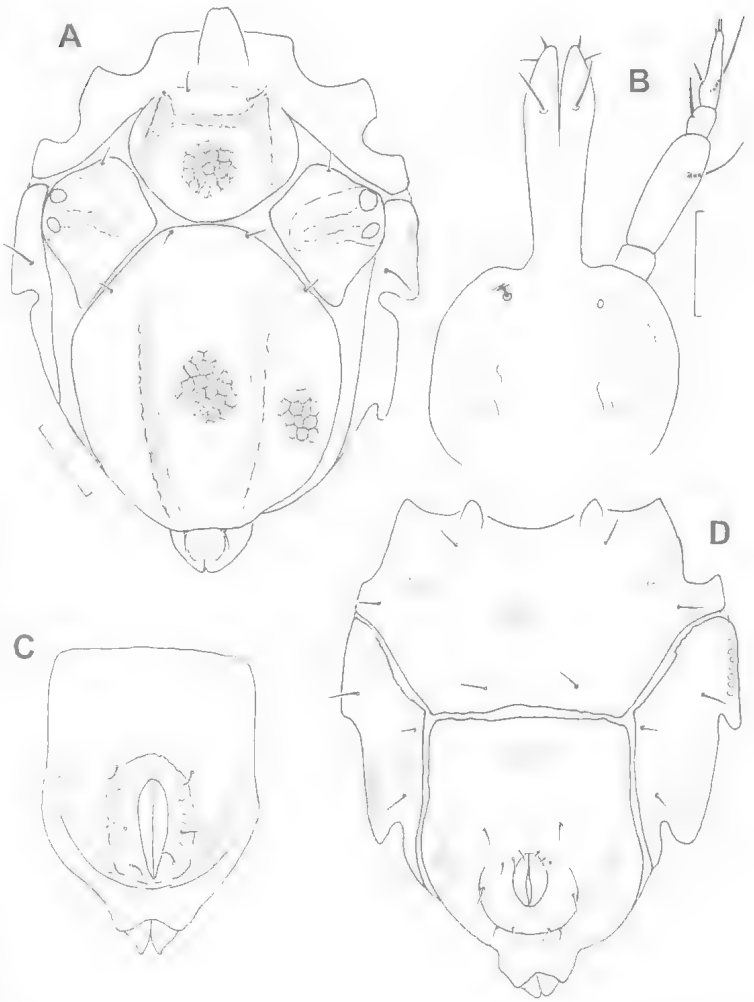



FIG. 9. *Agauopsis narinosa* sp. nov., adult: A, dorsal idiosoma; B, ventral gnathosoma; C, genitoanal plate of female; D, ventral idiosoma of male. Scale lines: A = 50μm, B = 25μm, C,D = 50μm.

*Female*. Idiosoma 350 long. Three pairs of pgs inserted as illustrated (Fig. 9C); areolae posterolaterlally to GO wider than in male.

REMARKS. *Agauopsis narinosa* sp. nov. belongs to the *microrhyncha* group (see Bartsch, 1986, 1996a). Species of this group can be recognised by the presence of 4 spiniform setae on tibia I, of which 2 are closely associated. Other species in that group are *A. antarctica* (Lohmann, 1907), *A. australiensis* Bartsch, 1996a, *A. crassipes* (Gimbel, 1920), *A. cryptorhyncha* (Trouessart, 1889a), *A. curvatus* Krantz, 1973, *A. felicis* Newell, 1984, *A. glacialis* Bartsch, 1993e, *A. humilis* Bartsch, 1992c, *A. insularis* Newell, 1984, *A. microrhyncha* (Trouessart, 1889b), *A. mokari* Otto, 1994, *A. paulensis* (Lohmann, 1907), *A. pusilla* Viets, 1950, *A. racki* Newell, 1984, *A. robusta* Sokolov, 1952, *A. similis*

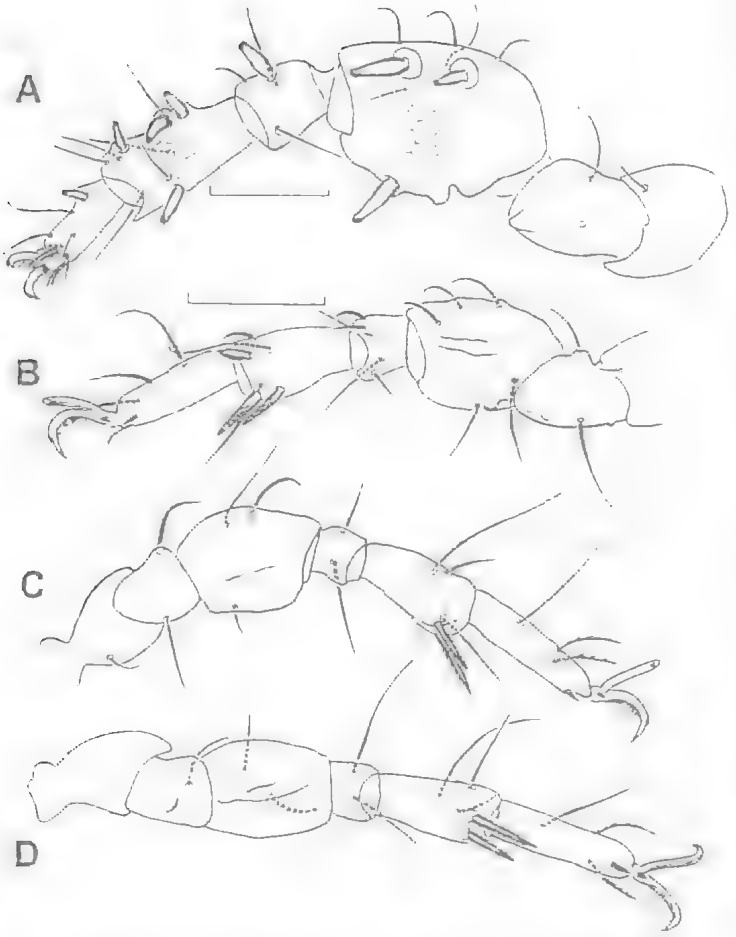



FIG. 10. *Agauopsis narinosa* sp. nov., adult: A, leg I, ventromedial; B, leg II, ventromedial; C, leg III, medial; D, leg IV, ventral. Scale lines =

Bartsch, 1979 and *A. vinae* Newell, 1984. In *A. narinosa* the frontal spine is conspicuously broad and truncated which among the species of the *microrhyncha* group is known only for *A. glacialis*. *Agauopsis narinosa* differs from *A. glacialis* by the narrower costae on the PD.

**Agauopsis okinavensis** Bartsch
(Fig. 11)

*Agauopsis okinavensis* Bartsch, 1986: 169.

MATERIAL. Great Barrier Reef Marine Park: ANIC, F, John Brewer Reef, 18°38.25'S 147°04.42'E, 11 Apr. 1998, coarse sand at 15m; QMS105194, F, Myrmidon Reef, back, 17°46.03'S 146°26.38'E, 6 Mar. 1998, L. Levantier, medium coarse sand at 7m; QMS105195, M, ZMH, M, Carter Reef, ca. 14.32°S 145.35°E, 11 Oct. 1998, coarse sand at 0.5m.

REMARKS. The specimens listed above are the first records of this species from Australia. It was previously known only from its type locality in Okinava.

Bartsch (1986) described 1 pair of ventral setae on the posterior epimeral plate and did not see pores on the posterodorsal plate whereas in the Australian specimens 3 pairs of setae and a pair of pores are present at the corresponding locations. Unfortunately, I have been unable to examine the type, as the specimen could not be found in the United States National Museum where it had been deposited (R. Ochoa pers. comm.). However, the presence of only 1 pair of ventral setae on the posterior epimeral plate would be highly unusual (all species in the genus possess 3 pairs) and I therefore regard it as more likely that either further 2 pairs were broken off and the insertions were overlooked or that the holotype is an abnormal specimen. The apparent lack of pores on the posterodorsal plate is also not a distinguishing character as these pores are often obscured.

The present material contains previously unknown males which differ from the female as follows.

*Male*. Idiosoma 412-432 long. GO surrounded by 24-30 pgs inserted between cuticular swellings (Fig. 11); all pgs branched in distal half. Pair of outlying setae inserted anterolateral to GO. GO with 5 pairs sgs, 3 pairs anterior and 2 pairs posterior.

**Agauopsis ripa** sp. nov.
(Figs 12,13)

ETYMOLOGY. Latin, *ripa* = coast, referring to the species' apparent restriction to coastal habitats.

MATERIAL. HOLOTYPE: QMS105196, M, Great Barrier Reef Marine Park, Toolakea Beach (near Townsville), ca. 19°09'S 146°35'E, 15 June 1997, algae and tubeworm colonies on boulders at low tide level. PARATYPES: Great Barrier Reef Marine Park: QMS105197-105200, 4F, ANIC

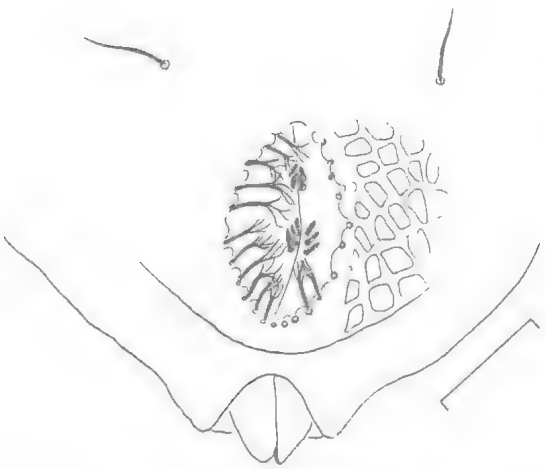


FIG. 11. *Agauopsis okinavensis* Bartsch, male: genitoanal plate. Scale line = 50μm.

M, ZMH M, data as for holotype; QMS105201, M, Townsville, Magnetic I., 16 Nov. 1996, algae at low tide; QMS105202, M, Cairns, Yorkeys Knob, 21 June 1997; QMS105204, F; QMS105203, M, Townsville, 17. Feb. 1997, intertidal algae on rocks; QMS105205, M, Townsville, 16 Feb. 1997, sediment between mangrove roots; QMS105206, M, Cape Ferguson (near Townsville), 19°16.09'S 147°03.05'E, 13 July 1997, algae on intertidal rocks; QMS105207-105209, 3M, Cape Hillsborough, 23 Dec. 1997, intertidal algae (mainly *Cladophora* sp.) around low tide mark. Southern Queensland: UQIC, M, 2F, Caloundra, Kings Beach, 20°00'S 148°16'E, 17 Aug. 1996, C.A. Bryant.

*Male*. Idiosoma 349-460 long (holotype 384). Three pairs of setae inserted in membranous cuticle between AD, OC and PD (Fig. 12A). AD rounded posterolaterally; frontal spine blunt and minute, in several specimens barely discernible; cuticle pierced by scattered canaliculi and with reticulate ornamention; slightly raised H-shaped areola pierced by canaliculi which are wider than those of rest of plate; canaliculi within areola not forming distinct groups; at the end of the anterior arms of H-shaped areola with widely separated pair of setae and at same level with pair of inconspicuous gland-pores. OC with 2 corneae borne on elevated transverse areola; with conspicuous canaliculi similar to those on H-shaped areola of AD; posterior and anterior of areola with reticulate ornamention and canaliculi similar to that on AD; pore just posterior to corneae at posterolateral margin of elevated areola. PD in most specimens slightly longer than wide, in some specimens length and width subequal; with pair of medial costae and pair of narrow marginal costae, each bearing canaliculi as described for AD; medial costae merging posteriorly to form 'U'; 1 pair of setae directly lateral to medial costae, in some specimens inserted on anterior half of plate, in other specimens half way along plate; another pair of setae at posterior margin of plate; between costae with reticulate ornamentation and fine canaliculi as described for AD. AE with posterior margin slightly concave (Fig. 12D); very faintly reticulate and pierced by canaliculi which are distributed somewhat more densely than on dorsum. Ventral PE with anterior seta much longer than posterior one; pierced by canaliculi similar to those of AE. GA with variable anterior margin, in some specimens rounded (Fig. 12B) in others more truncate; pierced by canaliculi similar to AE; pgs forming 2 circles, inner circle with 9-19 setae, outer circle with 19-40 setae; 1 pair of outlying setae near anterolateral margin of plate; 5 pairs of short and thick sgs, 2 pairs anteriorly and 3 pairs posteriorly, middle pair of 3 posterior setae distinctly larger than other 2 pairs.

Venter of gnathosomal base with pair of widely separated setae anteriorly (Fig. 12B); pierced by canaliculi to level of setae, except for area along median axis; canaliculi in circular scar on either side finer than on remainder. Rostrum surpassing palps. Palp segment P-3 with truncate apically denticulate spine, that spine slightly longer than P-3.

All segments pierced by canaliculi. Leg I (Fig. 13A) slightly heavier but not distinctly longer than other legs (Fig. 13B-D), with the following complement of heavy spines: 2 ventral and 2 medial on telofemur (the 2 ventral ones closer together), 1 ventral and 1 medial on genu, 1 ventral and 2 medial on tibia, 1 medial on tarsus, all relatively short and denticulate in distal half. Chaetotaxy (trochanter-tibia): I 1-2-9-5-9 (Fig. 13A), II 1-2-6-5-7(8)-5 (Fig. 13B), III 1-2-3-3-5-3 (Fig. 13C), IV 0-2-3-3-5-3 (Fig. 13D); distalmost medial seta on tibia II blunt and slightly bipectinate (Fig. 13B); 2 ventral setae on tibiae II-IV spiniform and denticulate (Fig. 13B-D), one specimen with 3 such setae on tibia II; 1 medial seta on tibia II bipectinate. Tarsus I with 2 unpaired ventral setae and pair of doubled pas; tarsus II lacking ventral seta but with 1 spur-like medial pas, 1 lateral double-pas (ventral member of double-pas <1/2 the length of dorsal member). Tarsi III and IV with 1 spur-like lateral pas. Tarsal claws I smooth, without pecten or accessory process, claws II-IV with pecten and accessory process. Median claw on tarsus I bidentate, on tarsi II-IV absent.

*Female*. Idiosoma 369-440 long. Position of 3 pairs of pgs as in Fig. 12C. Sgs absent.

REMARKS. *Agauopsis ripa* sp. nov. belongs to the *brevipalpus* group (see Bartsch, 1986) which occurs in all oceans, in cold as well as warm water areas. Species of this group possess reticulated dorsal plates, often an H-shaped areola on the AD, 3 spines on the tibia of the front legs, usually 3 (sometimes 2) pairs of dorsal setae in the dorsal membranous cuticle and lack ventral setae on tarsus II. Within this group *A. moorea* Bartsch, 1992, *A. atacamae* Newell, 1984, *A. borealis* Newell, 1947, *A. brevipalpus* (Trouessart, 1889b), *A. ibssi* Bartsch, 1996d, *A. littoralis* Bartsch & Iliffe, 1985, and *A. sordida* Bartsch, 1992c, possess 4 spines on telofemur I. *Agauopsis ripa* is distinguished from *A. moorea* by having 6 instead of 5 setae on telofemur II, from *A. atacamae* by having a much wider PD, from *A. borealis* by having the setae on the AD more widely separated, from *A. littoralis* by having 2 instead of 3 denticulate spiniform setae on tibiae III and IV, from *A. ibssi* by the presence of distinct costae on the PD, from *A. brevipalpus* by the relatively shorter spines on leg I and from *A. sordida* by the relatively longer rostrum.

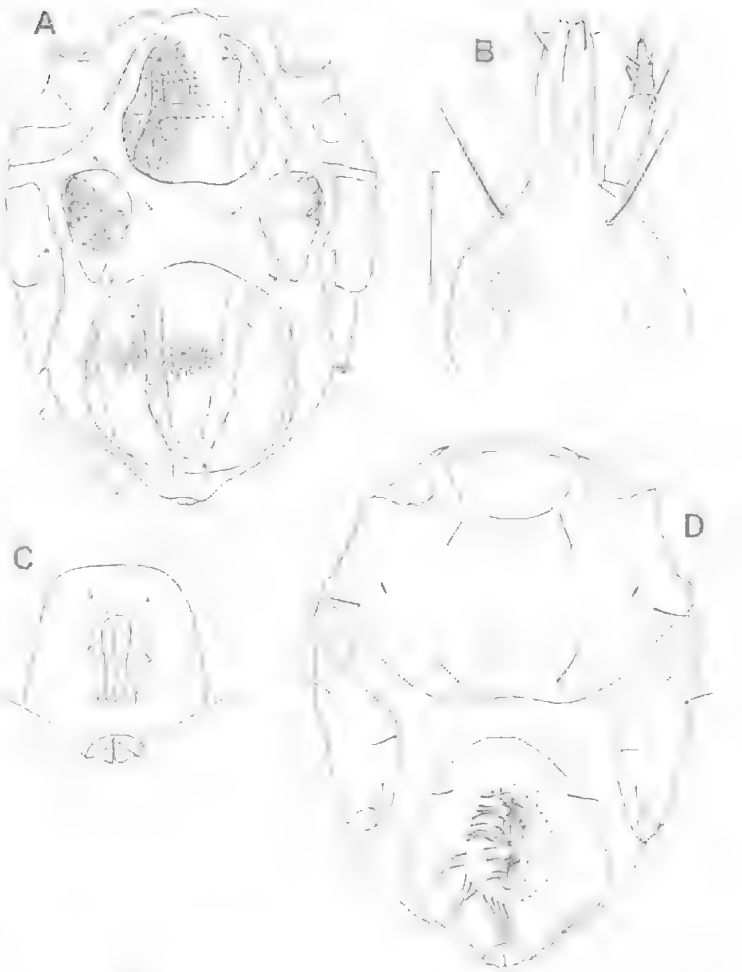



FIG. 12. *Agauopsis ripa* sp. nov., adult: A, dorsal idiosoma of male; B, ventral gnathosoma; C, genitoanalplate of female; D, ventral idiosoma of male. Scale lines: A = 100µm, B = 50µm, C,D = 100µm.

## KEY TO NAMED AUSTRALIAN SPECIES OF *AGAUOPSIS*

The following key includes all named *Agauopsis* species known to occur in Australia. A further 2 unnamed species, one of these previously erroneously identified as *Agauopsis similis* Bartsch, 1979 (see Bartsch, 1996a) are here not included. Also excluded from this key are *Agauopsis brevipalpus* (Trouessart, 1889b) and *A. microrhyncha* (Trouessart, 1889b). Both species have been recorded by Lohmann (1893) from Australia but the record of the former is a misidentification (Bartsch, 1996a), while the record of the latter is believed to be a lapse (Bartsch, 1996a). However, it is yet unknown whether the specimen Lohmann (1893) identified as *Agauopsis brevipalpus* is of an undescribed species or perhaps belongs to the Australian *Agauopsis ripa* sp. nov., which is very similar to *A. brevipalpus*.

1. Tibia I with 5 spines, 2 of these closely associated, AD as in Fig. 2A . . . . . *I. henzivi* sp. nov.
   Tibia I with 4 spines, 2 of these closely associated (Fig. 10A) . . . . . 2
   Tibia I with 3 spines, none closely associated (Fig. 5A) 4
2. Anterior edge of frontal spine truncate (Fig. 9A) . . . . . *A. narinosa* sp. nov.
   Frontal spine not distinctly truncate . . . . . 3
3. Telofemur I with 4 heavy spines [illegible] Otto, 1904
   Telofemur I with 3 heavy spines . . . . . *I. australiensis* Bartsch, 1996a
4. AE with garland-like ornamentation (Fig. 6B) . . . . . 5

AE without garland-like ornamentation . . . . . 7

5. Posterior to frontal spine a porous areola (Fig. 6A). . . . . *A. decorata* sp. nov.

Posterior to frontal spine pair of ridges (Fig. 7A). . . . 6

6. Costae on PD consisting of double row of rosette pores (Fig 7A); 1 small areola medial at posterior margin of AE (Fig. 7C); spine on P-3 heavy and blunt, with few denticles at tip . . . . . *A. fenneri* sp. nov.

Costae on PD consisting of single row of rosette pores; 2 small areolae medial at posterior margin of AE; spine on P-3 slender, tapering. . . . . *A. ornatella* Bartsch, 1996a

7. Palp segment P-4 as long as P-2 (Fig. 4B) . . . . . 8

Palp segment P-4 distinctly shorter than P-2 (Fig. 2D) . . . . . 9

8. Anterior epimeral plate reaching level leg IV insertions *A. okinavensis* Bartsch, 1986 . . . . . .

Anterior epimeral plate reaching only level of leg III insertions (Fig. 4A) . . . . . *A. capillosa* sp. nov.

9. PD with the 3 posterior pairs of setae much longer than anterior pair of seta . . . . *A. elaborata* Bartsch, 1996a

PD with all setae of subequal length (Fig. 2A) . . . . 10

10. AD with pair of setae posterolaterally; membranous cuticle greatly reduced and without setae . . . . . *A. aequilivestita* Bartsch, 1996a

AD without a pair of setae posterolaterally; membranous cuticle fairly extensive and with three pairs of setae (Fig. 12A). . . . . 11

11. AD fused to AE anteriorly, with H-shaped areola (Fig. 12A); telofemur I with 4 heavy spiniform setae (Fig. 13A) . . . . . *A. ripa* sp. nov.

AD and AE separated by membranous cuticle, without H-shaped areola; telofemur I with 1 heavy spiniform seta *A. collaris* Otto, 1994

## **Halacaropsis** Bartsch

*Halacaropsis* Bartsch, 1996a: 12.

TYPE SPECIES. *Agaue hirsuta* Trouessart, 1889b, by original designation.

DIAGNOSIS. Dorsal plates widely separated. Three pairs of dorsal setae inserted in striated integument, of these at least 2 much longer and heavier than the dorsal setae on AD and PD. Leg I with large spiniform setae on telofemur, genu, tibia and tarsus. Tarsi curved; with a heavy median claw. Tarsi III and IV each with 1 or 2 ventral setae.

### **Halacaropsis nereis** sp. nov.
(Figs 14,15)

ETYMOLOGY. Greek, *nereis* = a sea-nymph.

MATERIAL. HOLOTYPE: QMS105211, F, Great Barrier Reef Marine Park, Townsville, 16 Feb. 1997, coralline algae at low tide mark. PARATYPES: Great Barrier Reef Marine Park: QMS105212, 105213, 105216, 3M, ANIC M, ZMH M, QMS105217, F, data as for holotype; QMS105262, F, Townsville, 17 Feb. 1997, intertidal algae on rocks; QMS105263, 105214, 2F, QMS105264 M, Cairns, Yorkeys Knob, 21 June 1997, intertidal algae & mussels; QMS105265, F, QMS105210 M, Cape Hillsborough, 23 Dec. 1997, intertidal algae (mainly *Cladophora* sp.) around low tide mark.

*Male*. Idiosoma 555-648 long; all plates with smooth cerotegumental membrane; 3 setae in membranous cuticle much longer and heavier than other dorsal setae (Fig. 14A). AD and AE fused anteriorly; anterior margin with inconspicuous frontal spinelet; posterolateral part pierced by canaliculi; anterolaterally with pair of setae and pair of gland pores. OC distinctly longer than wide; anterolaterally with 2 corneae borne on slight elevation; pierced by canaliculi except for elevation and posterolateral margin; posterior to corneae a pore and a canaliculus. PD with 2 longitudinal areolae pierced by canaliculi; 1 pair of small setae in posterior half; posterior margin thickened medially. Adanal setae on anal cone. AE with 3 pairs ventral setae and pair of epimeral pores (Fig. 14E). GA with 2 circles of pgs, inner circle with ca. 10-12 setae, outer circle with ca. 33-39 setae; further pair of outlying setae near anterior margin of GA. GO with 5 pairs of peg-like sgs and 1 pair of heavier sgs with thickened base (Fig. 14D).

Ventral gnathosomal base smooth. Rostrum about as long as gnathosomal base (Fig. 14C). P-3 with apically denticulate spine; P-4 with 6 setae as illustrated (Fig. 14B).

Leg I with the following arrangement of heavy spiniform setae: 1 ventral and 2 medial on telofemur, 1 ventral and 1 larger medial on genu, 1 ventral and 2 medial on tibia, 1 medial on tarsus (Fig. 15A). Chaetotaxy (trochanter-tibia): I 1-3-8-9-11 (Fig. 15A), II 1-4-7-7-11 (Fig. 15C); III 3-2-5(4)-6-9 (Fig. 15D); IV 3-2-5-6-9 (Fig. 15F). Leg II with 2 denticulate spiniform setae (Fig. 15C), tibiae III and IV each with 1 such seta, proximal to these on tibiae III and IV with slightly thickened but smooth seta (Fig. 15 D,F,G). Paired claws on all tarsi smooth. Median claw on tarsus I slightly bidentate (Fig. 15B), on tarsi II-III unidentate (Fig. 15E); median claws of tarsi II-IV larger than those of tarsus I.

*Female*. Idiosoma 574-698 long (holotype 690). GO surrounded by 10-11 pgs (Fig. 14E); 5 pairs of small sgs.

*Abnormalities*. One of the legs I in some specimens has 4 spiniform setae on the tibia or 3 spiniform setae on the genu, while the other leg I in the same specimens showed the normal complement of spiniform setae.

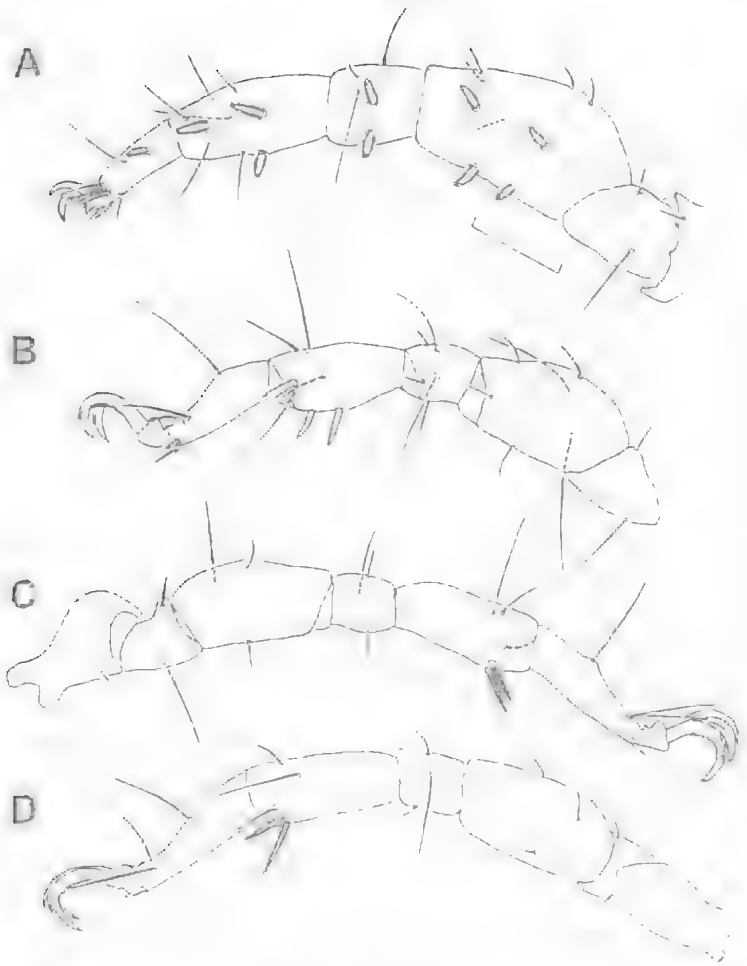



FIG. 13. *Agauopsis ripa* sp. nov., adult: A, leg I, medial; B, leg II, medial; C, leg III, medial; D, leg IV, medial. Scale lines = 50μm.

REMARKS. At present 4 other species of *Halacaropsis* are known: *H. capuzina* Bartsch, 1996a, *H. hirsuta* (Trouessart, 1889b), *H. warringa* Otto, 1993, and an unnamed species *Halacaropsis* sp. which was previously misidentified by Lohmann (1909) as *H. hirsuta* (see Bartsch 1996a). *Halacaropsis nereis* differs from its congeners by having smooth claws on all legs and a unidentate median claw on legs II-IV. It can also be distinguished from *H. warringa* and *H. capuzina* by having only 1 denticulate seta on tibia IV (versus 2 and 3 such setae in *H. warringa* and *H. capuzina* respectively) and from *Halacaropsis* sp. by having 3 pairs of heavy setae on the dorsum instead of 2 pairs (see Bartsch 1996a).

## CONCLUSIONS

Of the 13 named and 2 unnamed species of *Agauopsis* which are certain to occur in Australian waters (excluding *Agauopsis brevipalpus* and *A. microrhyncha*, see under 'Key to named Australian species'), 3 were only found on the temperate southeastern coast of Victoria and New South Wales (*A. collaris* Otto, 1994, *A. mokari* Otto, 1994 and *Agauopsis* sp. Bartsch, 1996a), 6 in the GBR region (those newly described in the present paper) and 4 only on Rottnest I. in SW Australia (*A. australiensis* Bartsch, 1996a, *A. elaborata* Bartsch, 1996a, *A. ornatella* Bartsch, 1996a and *Agauopsis* sp. Bartsch, 1996a). Similarly, each of these regions has their own species of *Halacaropsis*: *H. capuzina* Bartsch, 1996a on Rottnest I., *H. nereis* sp. nov. on the GBR and *H. warringa* Otto, 1993, in SE Australia. A fourth undescribed species of this genus previously identified by Lohmann (1909) as *Halacaropsis hirsuta* (see Bartsch, 1996a) was found at Shark Bay in Western Australia. Thus it appears that the halacarid fauna of each of these regions is distinctly different from one another. However, 1 species (*A. aequilivestita*) occurs both on Rottnest I. as well as on the GBR indicating that some links exist between the fauna of both regions. It is yet unknown whether the species from the GBR also occur in neighbouring tropical regions as very little collecting has been done in the western part of the South Pacific. However, at least 1 species, *Agauopsis okinawensis*, is not endemic to the GBR region.

The genera *Agauopsis* and *Halacaropsis* only represent a small part of halacarid species usually found during surveys. For example, of 88 species found during a survey of Rottnest island only 5 belonged to the genus *Agauopsis* (Bartsch, 1996a), representing ca. 5.7% of all halacarids described from the island. Projecting this number

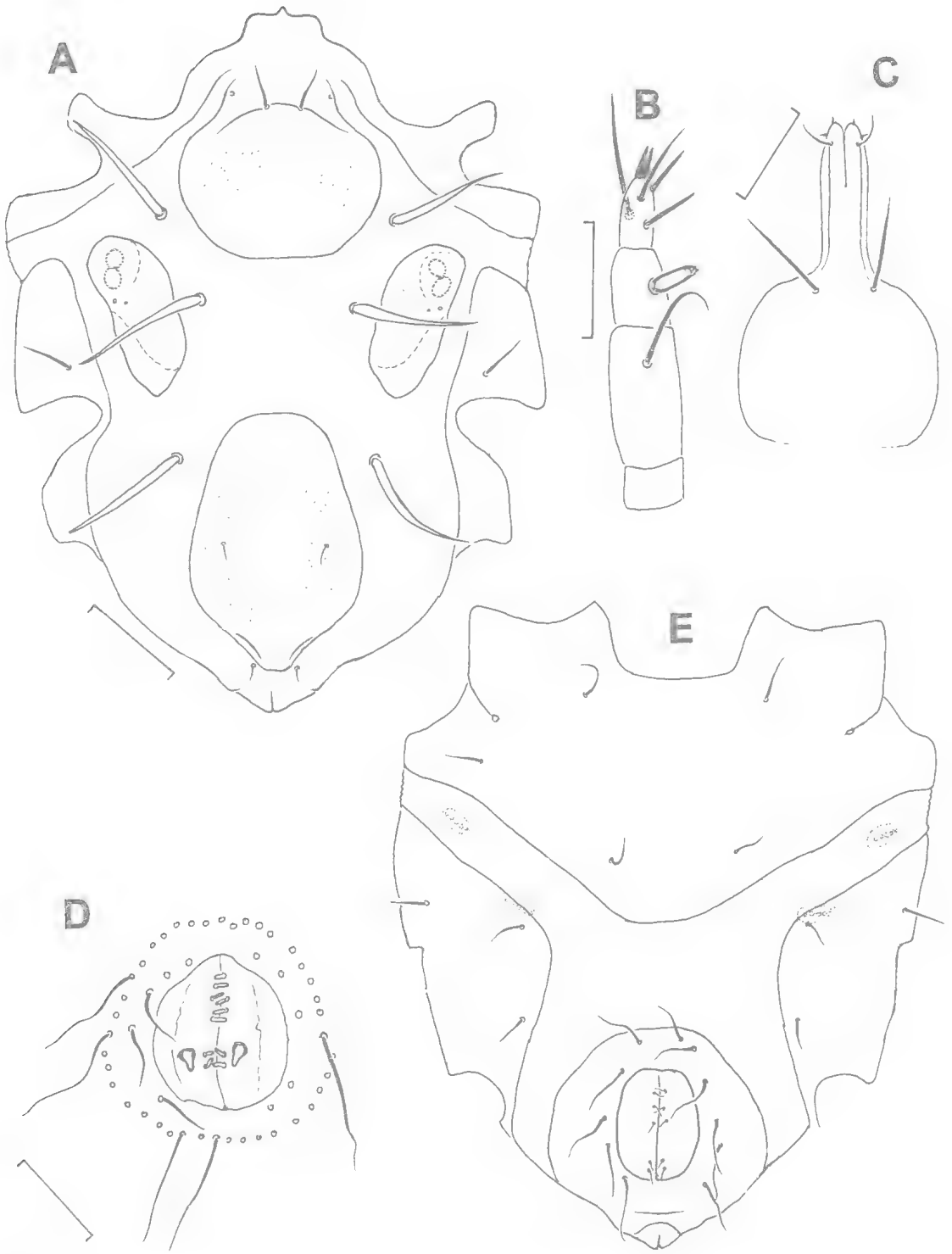



FIG. 14. *Halacaropsis nereis* sp. nov., adult: A, dorsal idiosoma; B, palp, dorsal; C, ventral gnathosomal base and rostrum; D, genital opening of male; E, ventral idiosoma of female. Scale lines: A = 100μm; B-D = 50μm; E = 100μm.

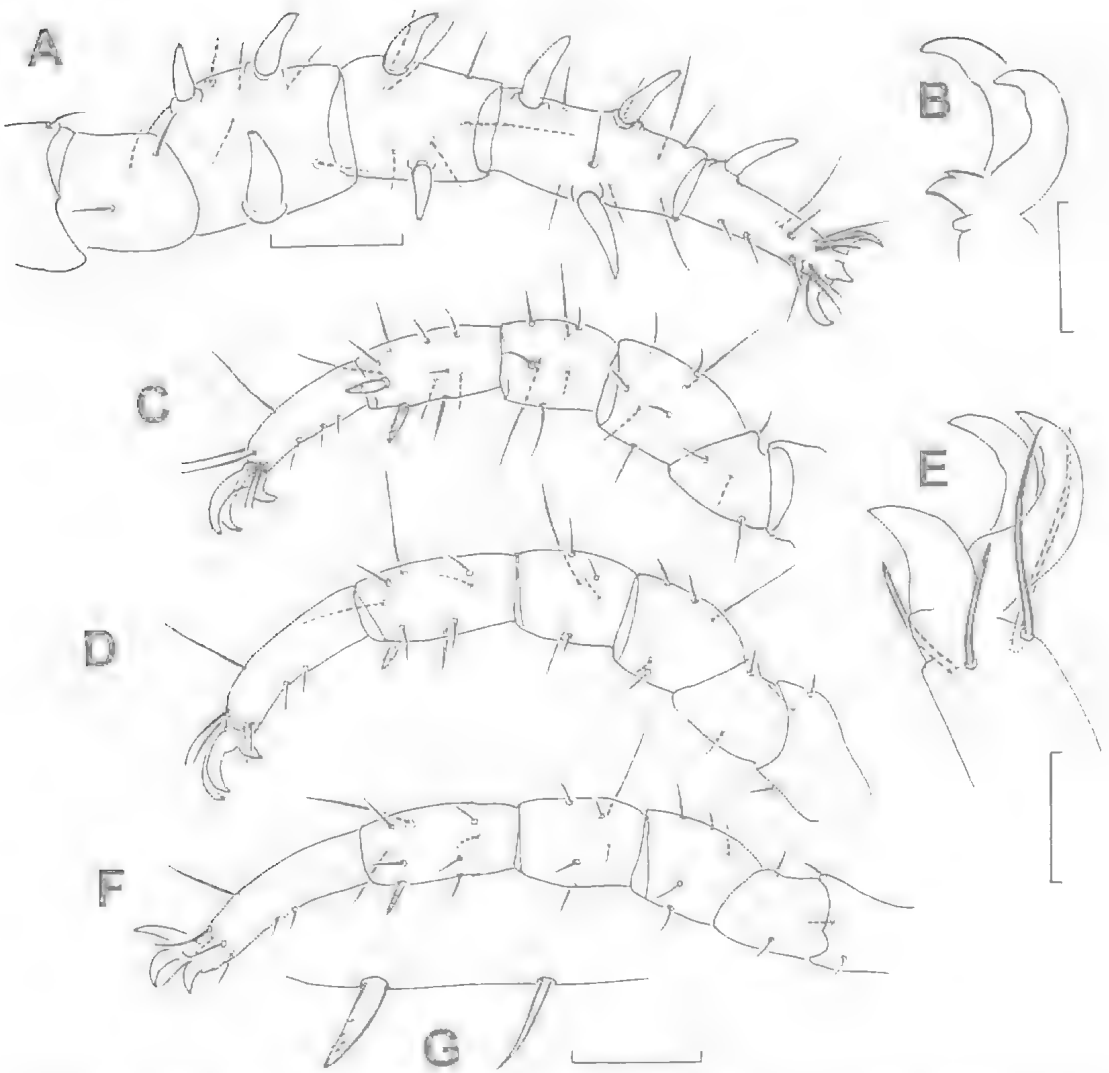



FIG. 15. *Halacaropsis nereis* sp. nov., adult: A, leg I, ventral; B, tarsal claws of leg I; C, leg II, medial; D, leg III, medial; E, tarsal claws of leg III; F, leg IV, lateral; G, enlarged aspect of ventral tibia IV. Scale lines: A,C,D,F = 100μm; B,E,G = 25μm.

onto the GBR region from where now 8 species of *Agauopsis* are known, and taking into account that only few parts of the region have yet been surveyed, it may be estimated that the total number of halacarid species in that area may easily exceed 140 species.

## ACKNOWLEDGEMENTS

I thank the Australian Biological Resources Study (ABRS) for funding the present project and the Australian Institute of Marine Science for providing me with all necessary facilities and laboratory space. I am grateful to John Benzie for giving me his continuous support for this project, the Great Barrier Reef Marine Park Authority for giving permission to collect halacarid mites and Dave Walter and Greg Daniels (University of Queensland), Eva Karl and M. Grasshoff (Forschungsinstitut und Naturmuseum Senckenberg), Mark Harvey (Western Australian Museum), Michel Naudo (Muséum National d'Histoire Naturelle) and Ilse Bartsch (Biologische Anstalt Helgoland) for the loan of specimens. Special thanks to Ilse Bartsch for supplying much of the relevant literature and to her, John Benzie, Kate Wilson and two

anonymous referees for comments on the manuscript. I am also indebted to Katharina Fabricius and Paula Tomkins for giving me the opportunity to participate on their field trips, and Peter Doherty, Doug Fenner and Guillermo Diaz-Pulido for providing specimens from the Coral Sea reefs. This publication is contribution 938 of the Australian Institute of Marine Science.

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# REVIEW OF THE MYGALOMORPH GENUS *MELLOINA* BRIGNOLI (PARATROPIDIDAE: ARANEAE)

ROBERT J. RAVEN

Raven, R.J. 1999 06 30: Review of the mygalomorph genus *Melloina* Brignoli (Paratropididae: Araneae). *Memoirs of the Queensland Museum* **43**(2): 819-825. Brisbane. ISSN 0079-8835.

The South American spider genus *Melloina* Brignoli, 1985 is reviewed. The type species, *Melloina gracilis* (Schenkel, 1953) is redescribed and a new species *M. rickwesti* is named from Panama. ❐ *Mygalomorphae, Paratropididae, Melloina, taxonomy, Venezuela, Panama.*

*Robert J. Raven, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 15 April 1998.*

The enigmatic Venezuelan genus *Melloa* Schenkel, 1953 was first placed in the Theraphosidae where its remarkable absence of dense hair on the legs, carapace and abdomen set it well aside from other taxa. In a cladistic analysis of all mygalomorphs, Raven (1985) transferred the genus to the Paratropididae and discussed the transfer in detail. The cladogram of Goloboff (1993) was not at variance with that.

The paratropidids are sparsely setose glabrous spiders which make no formal burrow but hide in the surface layers of the soil (West, pers. comm.). Their entire cuticle is soil-encrusted, the eye tubercle is very strongly arched and elevated, thick peglike setae are placed sparsely across the abdomen and the trichobothria are set in shallow protective cuticular cradles on the tibiae (Raven, 1985, figs. 165-7, 169, 171-2, 174). These characters no doubt are all sensory triggers for invertebrates moving across the soil.

Nomenclaturally, *Melloa* was blessed thrice. Both Brignoli (1985), in preparing his catalogue and Raven (1985) in his mygalomorph monograph noted the genus name was preoccupied and each proposed different replacement names, *Melloina* and *Glabropelma*, respectively. Brignoli was published earlier, thus his proposed genus name has precedence. However, Raven (1985) also proposed a family-group name Glabropelmatinae which is also valid. Goloboff (1995) incorrectly used the name *Glabropelma* in discussions and cladograms.

The new material presented here was taken during the IXth International Congress of Arachnology, in Panama.

The methods are those used in my previous papers (e.g. Raven, 1994). Micrographs were taken with a Polaroid Microcam. Measurements are in millimetres.

## Family PARATROPIDIDAE
## Subfamily GLABROPELMATINAE Raven, 1985
## **Melloina** Brignoli, 1983

*Melloa* Schenkel, 1953: 3; Brignoli, 1983: 138; Raven, 1985: 122, 155. Type species by original designation, *Melloa gracilis* Schenkel, 1953.

*Melloina* Brignoli, 1985: 380 (replacement name for *Melloa* preoccupied in Opilionida by *Melloa* Roewer, 1930); Platnick, 1989: 112; 1993: 115; 1998: 171.

*Glabropelma* Raven, 1985: 70, 122, 156 (duplicated replacement name for *Melloa* Roewer, 1930), figs. 16, 17; objective synonym of *Melloina*; Platnick, 1989: 112; Goloboff, 1995: 1-189.

DIAGNOSIS. *Melloina* differs from other paratropidid genera in the presence of distinct claw tufts on the legs and female palp, albeit thin on all, a normally (not highly) elevated eye tubercle and longer maxillary lobes than in the Theraphosidae but shorter than those in the Paratropidinae (Raven, 1985).

DESCRIPTION (supplementary to Raven, 1985). Tarsal organ low, domed. Leg cuticle smooth with band of finely fimbriate prostrate hairs beside dorsal midline of tarsi (Raven, 1994, fig. 19A).

DISTRIBUTION. Venezuela and Panama.

### **Melloina gracilis** (Schenkel, 1953) (Figs 1, 2)

*Melloa gracilis* Schenkel, 1953: 4, fig. 4a-c; Brignoli, 1983: 138.

*Melloina gracilis*: Brignoli, 1985: 380; Platnick, 1989: 112.

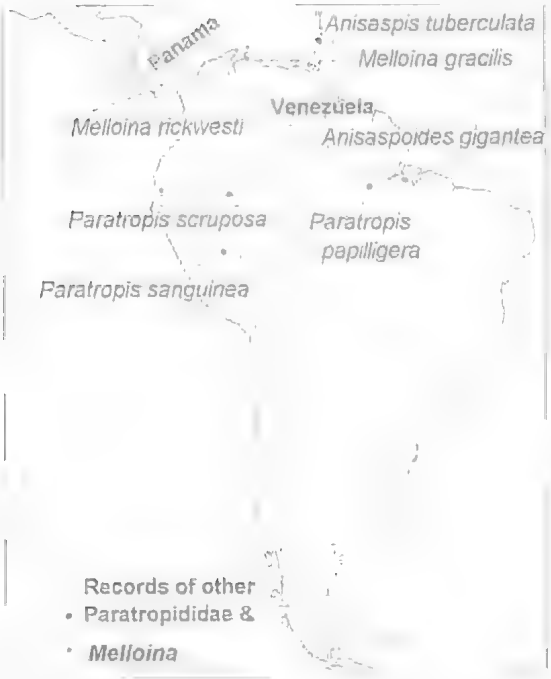



FIG. 1. Occurrence of *Melloina* and other Paratropididae.

*Glabropelma gracilis*: Raven, 1985: 122; Platnick, 1989: 112.

MATERIAL. HOLOTYPE: Male, El Pozon, Dto. Acosta, Prov. Falcon, Venezuela, Nov-Dec 1924, K. Wiedenmeyer, Naturhistorisches Museum, Basel, examined.

DIAGNOSIS. Differs from *M. rickwesti* in the more spinose tarsi and the presence of a tarsal crack on both legs III and IV (not only on IV).

DESCRIPTION. Holotype male. Carapace 8.40 long, 6.72 wide. Abdomen 8.24 long, 3.84 wide. Total length, 19.

*Colour in alcohol*. Carapace and legs red brown. Abdomen dorsally brown with 3 faint pallid lenticular areas; pallid ventrally.

*Carapace*. Glabrous, short, thornlike bristles on interstrial ridges; lateral margins with stout bristles in 1 row. Clypeus absent. Two bristles between PME; few fine on clypeal edge; none in striae. Fovea broad, procurved. Caput elevation low but above thorax.

*Eyes*. Tubercle raised, distinct. Group occupies 0.4 of head-width. Two rows; front row procurved, back row recurved. Eye group front width, back width, length, 73:79:33. MOQ front width, back width, length, 35:51:32. AME:ALE:PME:PLE, 27:18:16:14. AME-AME, 7, AME-ALE, 8, PME-PLE, 3, PME-PME, 32, ALE-PLE 5.

TABLE 1. Leg measurements of *Melloina gracilis*, holotype male.

| | I | II | III | IV | Palp |
|---|---|---|---|---|---|
| Femur | 7.83 | 7.17 | 6.50 | 8.67 | 4.67 |
| Patella | 4.50 | 4.00 | 3.33 | 3.83 | 2.83 |
| Tibia | 7.33 | 5.67 | 4.50 | 8.00 | 4.33 |
| Metatarsus | 6.67 | 6.00 | 6.50 | 10.33 | |
| Tarsus | 4.00 | 4.00 | 3.83 | 4.50 | 1.50 |

*Chelicerae*. Pilosity sparse with transverse ridges, only dorsal and fine setae laterally. Narrow, rounded, Rastellum absent. Fang long. Stridulatory strikers absent; no modifications but dark with pallid oval area near fang tip on groove not on interface. Furrow promargin with 15 large and 2 small teeth; intermedial row with 10 small and 30 fine, none on retromargin.

*Labium*. 1.76 wide, 0.88 long. With 60-70 blunt cuspules on anterior edge (see figure); long bristles; angled. Labiosternal suture a broad groove with two separated sigilla evident.

*Maxillae*. 2.40 long in front, 2.96 long behind, 1.40 wide; trapezoidal with conical inner edge not well defined; with *ca.* 60-70 cuspules spread, almost back onto heel but for more than half of maxillary length, blunt, spaced, not on mound. Heel angular; anterior lobes distinct, produced, angular. Lyra absent. Serrula absent.

*Sternum*. 3.96 long, 3.36 wide. Pilosity: fine hairs near margin, thick setae inside; rebordered slightly anteriorly. Sigilla oval: posterior 0.44 long, 0.32 from edge; middle 0.28 long, 0.16 from edge; anterior 0.12 long, 0.20 from edge.

*Legs*. Only bristles and spines evident; cuticle encrusted with soil. Tibia I with large truncated distal spur on proventral edge; an ovoid or leaf shaped megaspine on lower distal corner and digitiform megaspine on upper outer face of spur. Large trianguloid blunt upper process with digitiform tapering megaspine as long as process. No true scopula. Metatarsi and tarsi I, II with short hairs ventrally. Preening combs absent. Femora III noticeably incrassate. Tarsi III, IV ventrally cracked at *ca.* midpoint (see Table 1 for measurements).

*Spines*. Tarsi also with short thornlike setae. Leg 1, fe p4, d6, pa 0, ti p3, v13 + megaspines, me p2, v12, ta v9+9 in two straight rows; leg 2, fe p3, d5, pa 0, ti p3, v12, me p2, v11; ta v9+9 in two straight rows; leg 3, fe p4, d4, r5, pa 0, ti p2, d2, r3, v7, me p4, d1, r3, v11, ta v11+9 in two rows;

leg 4, fe p3, d6, r3, pa 0, ti p3, d2, r3, v10, me p4, d2, r3, v10, ta v11+12 in two rows; palp, fe p1, d3, ti p3, v6; ta 8 on larger lobe, 2 on smaller.

*Claws*. 4-5 short teeth on medial keel of paired claws of I; claw similar on IV but shorter. Small, weak, divided but distinct claw tufts.

*Trichobothria*. In two rows, each of *ca*. 9 on tibiae from half of curving row; irregular line of 15-20 on metatarsi; irregular band of 20-30 filiform and clavate on tarsi.

*Palp*. Bulb pyriform; embolus long, tapering to broad tip; cymbium of two dissimilar lobes. Tibia with shallow distoventral groove.

*Spinnerets*. PMS 0.40 long, 0.16 wide and apart, *ca*. 0.24 of basal PLS in diameter. Basal, middle, apical, and total articles of PLS, 0.80, 0.64, 0.84, 2.28, long respectively.

DISTRIBUTION. El Pozon, Venezuela.

REMARKS. This description differs from that of Schenkel (1953) in which sparse hairs on tarsi I and II are described as a scopula, even though the scopulate hairs are widely spaced. Differences in leg lengths may simply reflect minor differences in the points measured by Schenkel compared to the points I used (see Raven, 1994).

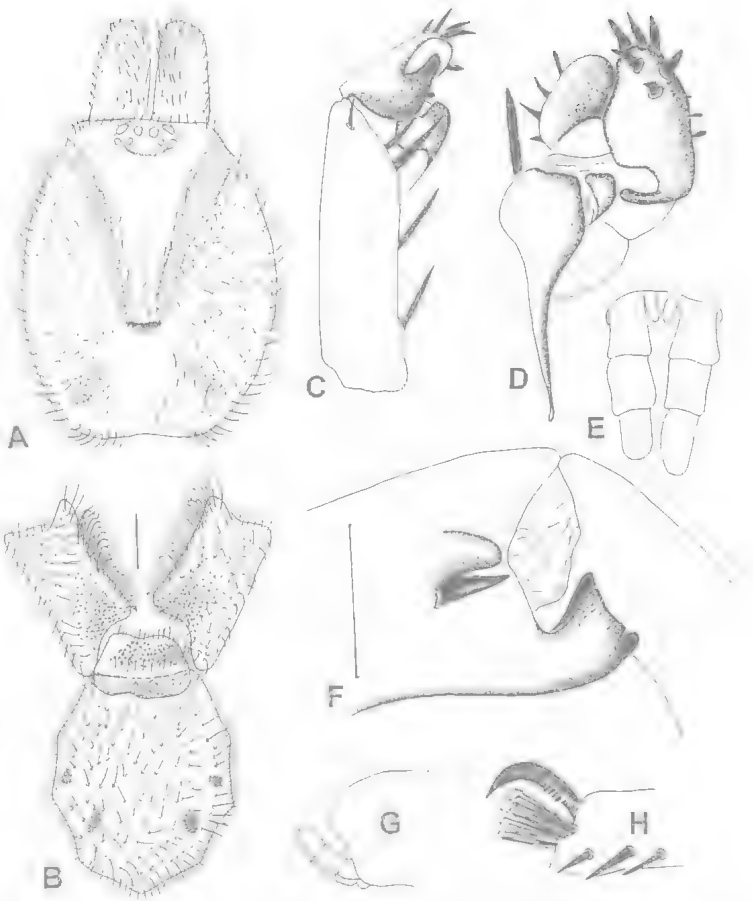



FIG. 2. *Melloina gracilis* Schenkel, holotype male. A, carapace & chelicerae, dorsal view. B, sternum, maxillae and labium, ventral view. C, palpal tibia, tarsus and bulb, prolateral view. D, palpal tibia, tarsus and bulb, proventral view. E, spinnerets, ventral view. F, tibia and metatarsus I, showing theraphosoid spur and megaspines, prolateral view. G, abdomen and spinnerets, lateral view. H, tarsus III, claws and tufts, prolateral view. Scale line on A = 2mm, B = 1mm, C-E, H = 0.5mm, G = 4mm, F = 1mm.

**Melloina rickwesti** sp. nov.
(Figs 1, 3-5)

*Melloina* sp: Raven, 1994: 322, fig. 19A.

ETYMOLOGY. For Rick West, student of tarantula taxonomy and biology, and the collector.

MATERIAL. HOLOTYPE: QMS6740, F, Limbo Camp, Gamboa, Panama, August 1983, Rick West. QMS34654, Penultimate M, same data but 25 Mar 1984, A. Decae.

DIAGNOSIS. Differs from *M. gracilis* in having only 2 rows each of 4 (cf. 9-12) spines on ventral tarsi, only tarsi IV (*cf.* III and IV) cracked, and a relatively shorter sternum and larger labium.

DESCRIPTION. Holotype female QMS6740. Carapace 4.64 long, 3.76 wide. Abdomen 5.04 long, 2.72 wide. Total length, 12.

*Colour in alcohol*. Carapace orange brown, striae and chelicerae darker, legs lighter. Abdomen dorsally brown with 2 pale paired areas anteriorly and generally with finely reticulated pallid areas. Sternum & labium orange brown, maxillae & other coxae lighter; abdomen ventrally pallid.

*Carapace*. Glabrous; lines of thick bristles along strial edges: *ca*. 5 along each caput edge, 3-4 on prolateral edges of lateral striae; 3 long and 2-3 small on outer edge of posterior striae. 6-8 behind

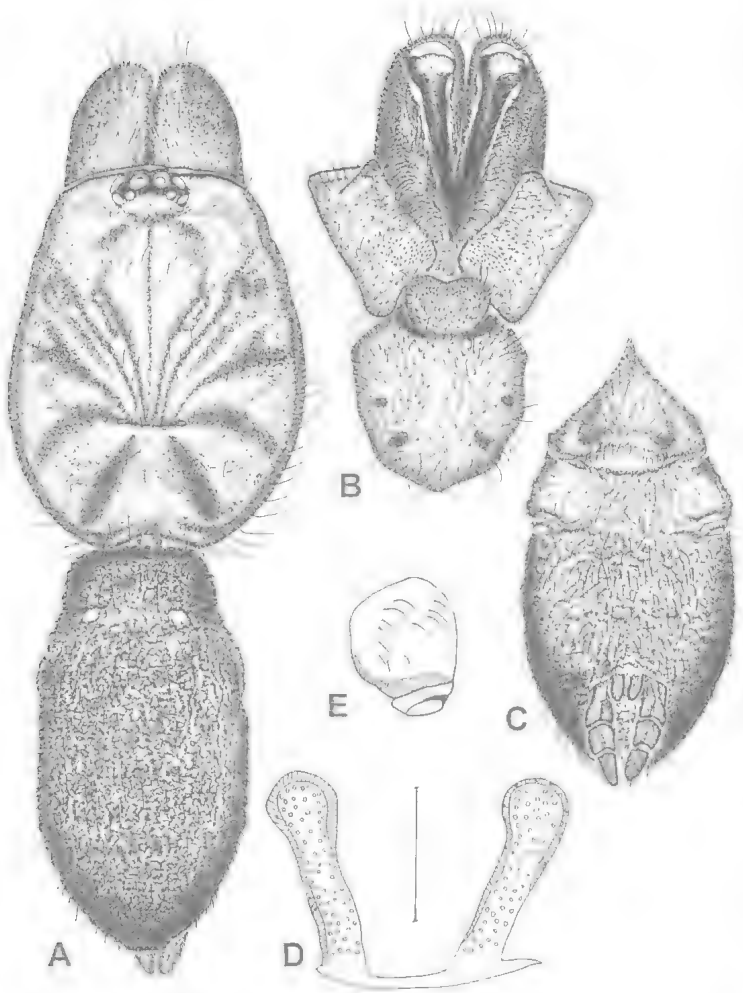



FIG. 3. *Melloina rickwesti* sp. nov., holotype female. A, carapace, chelicerae and abdomen, dorsal view. B, sternum, maxillae and labium, ventral view. C, abdomen and spinnerets, ventral view. D, spermathecae. E, book-lung, ventral right, ventral view. Scale line for A-C = 1.8mm, D = 0.25mm, E = 3.6mm.

PME; 4 between PME; 3 long recurved between AME and 2 long projecting from tubercle edge. Lateral margins with single line of thin (anterior part of carapace) to thick (mid-length of carapace posteriorly) bristles. Fovea short, slightly procurved. Clypeus absent.

*Eyes*. Tubercle low, well defined; anterior edge is carapace edge. Front row slightly procurved, back row recurved. PME pearly white, other eyes translucent. Group occupies 0.38 of head-width. Eye group front width, back width, length, 53:50:22. MOQ front width, back width, length, 22:33:16. AME:ALE:PME: PLE, 10:16:7:9. AME-AME, 0.6, AME-ALE, 0.5, ALE-ALE, 0.2, PME-PLE, 0.3, PME-PME, 2.0, ALE-PLE 0.2.

*Labium*. 1.16 wide, 0.80 long. Broad, rounded, deeply indented anteriorly. *ca*. 90 cuspules; cuspules largest on anterior slopes of lateral lobes; cuspules smallest along posterior edge where they equal size of cuspules on maxillae.

*Maxillae*. 1.68 long in front, 2.00 long behind, 1.12 wide. Placement and size of cuspules (*ca*. 60) uniform. Heel slightly produced; anterior lobe distinct.

*Chelicerae*. 3 distinct lines of setae dorsally, medialmost line has longest setae. No modified setae on interfaces. Promargin with long row of 14 large teeth interspersed with 3 smaller; intermedial region in basal one-third with *ca*. 30 very small pointed teeth and few larger teeth.

*Sternum*. 2.24 long, 2.48 wide. Rounded; strong setae around margins shorter, medial setae shorter. Cuticle lightly soil-encrusted. Sigilla small, oval, marginal.

*Legs*. Glabrous; covered only with thick and thin erect bristles. Anterior face of trochanter III and, to a lesser extent, IV with distinct basal invagination. All coxae soil-encrusted ventrally. Only tarsi IV cracked. Basifemoral thorns, thorn

TABLE 2. Leg measurements of *Melloina rickwesti*, holotype female.

| | I | II | III | IV | Palp |
|---|---|---|---|---|---|
| Femur | 3.60 | 2.96 | 2.72 | 4.48 | 2.64 |
| Patella | 2.16 | 1.84 | 1.44 | 1.84 | 1.60 |
| Tibia | 2.88 | 2.08 | 1.76 | 3.28 | 1.84 |
| Metatarsus | 2.16 | 2.00 | 2.16 | 3.52 | —— |
| Tarsus | 1.36 | 1.44 | 1.68 | 2.00 | 1.84 |
| Total | 12.16 | 10.32 | 9.76 | 15.12 | 7.92 |

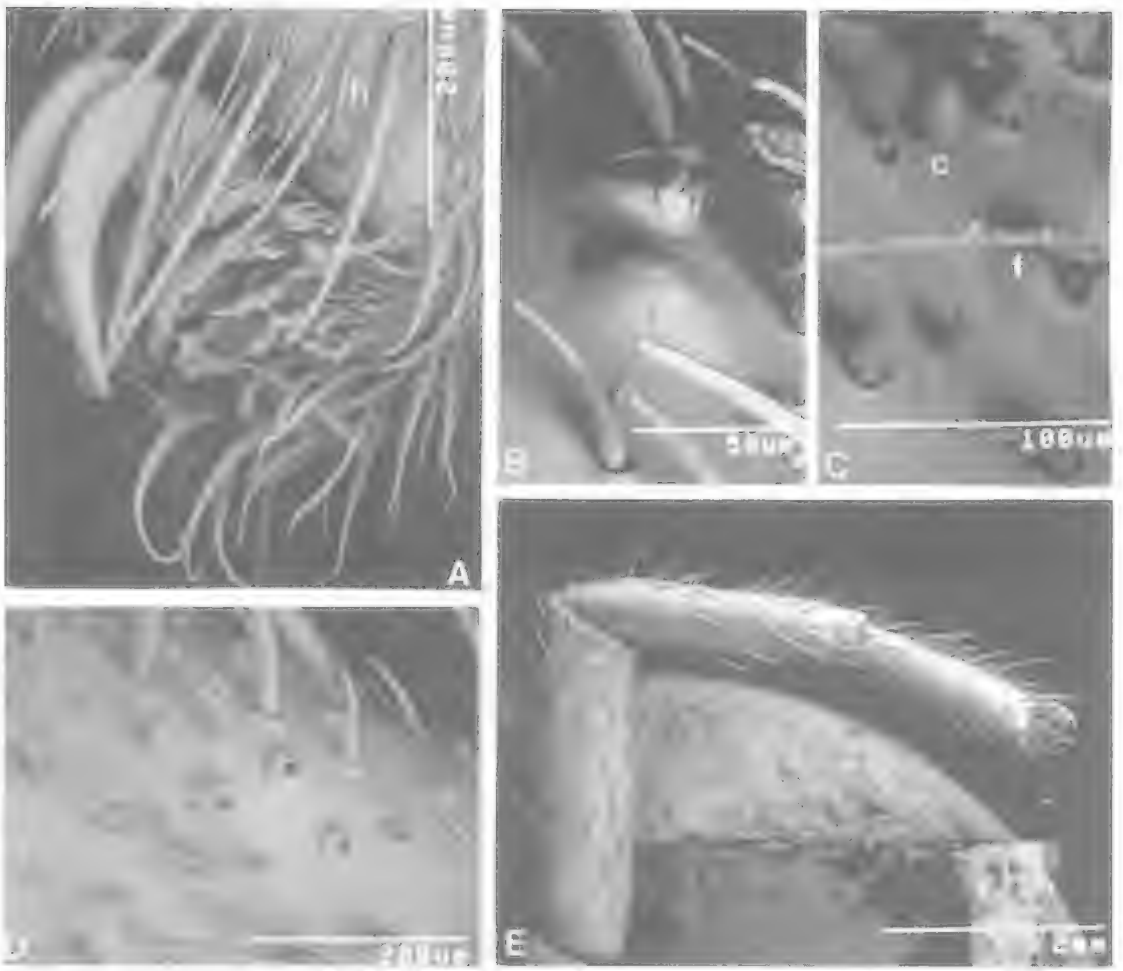



FIG. 4. *Melloina rickwesti* sp. nov., holotype female, scanning electron micrographs. A, claws, tufts and fimbriate hairs (h), paraxial view. B, tarsal organ, retrolateral view. C, cuticle of tarsus, showing filiform (f) and clavate (c) trichobothria, dorsal view. D, trichobothrial distribution on tarsi. E, patella, tibia, metatarsus, and tarsus, I, prolateral view.

spines, and metatarsal preening combs absent (see Table 2 for measurements).

*Spines*. Single spine dorsally on tarsi III and distal of crack on IV. Leg 1, fe p1, d2, pa 0, ti v5, me v8, ta v9; leg 2, fe p1, d4, pa 0, ti p1, v4, me p1, v6; ta v8; leg 3, fe p3, d3, r3, pa 0, ti p2, d2, r1, v7, me p3, r3, v8, ta v11; leg 4, fe d5, r1, pa 0, ti p2, r3, v7, me p4, r5, v9, ta v13 in two rows; palp, fe p1, d4, ti v6; ta v14.

*Claws*. 2 short claws with 2 small teeth on I and on IV but longer claws. Tufts deep, paired on palp and I, very thin on IV.

*Trichobothria*. In two rows, each of *ca*. 8 short trichae on tibiae, bases not saddlelike but straddled by irregular line of short translucent spathulate hairs and each of two distal trichobothrial bases ringed by these hairs. Similar on metatarsi, 4-5 trichae on retrolateral face proximally flanked by short clavate hairs, trichae on dorsal surface more distally. Tarsi dorsally with *ca*. 13 short filiform trichae in band interspersed with *ca*. 10 short clavate for length of tarsi.

*Booklung apertures*. Oval and sclerotised.

*Spinnerets*. *ca*. 10 distinct large (?pumpkiniform) spigots on PMS; small spigots barely discernible ventrally on PLS. PMS 0.40 long, 0.12 wide, 0.08 apart, *ca*. 0.70 of basal PLS in diameter. PLS length of basal, middle, apical, and total articles, 0.64, 0.40, 0.48, 1.52, respectively.

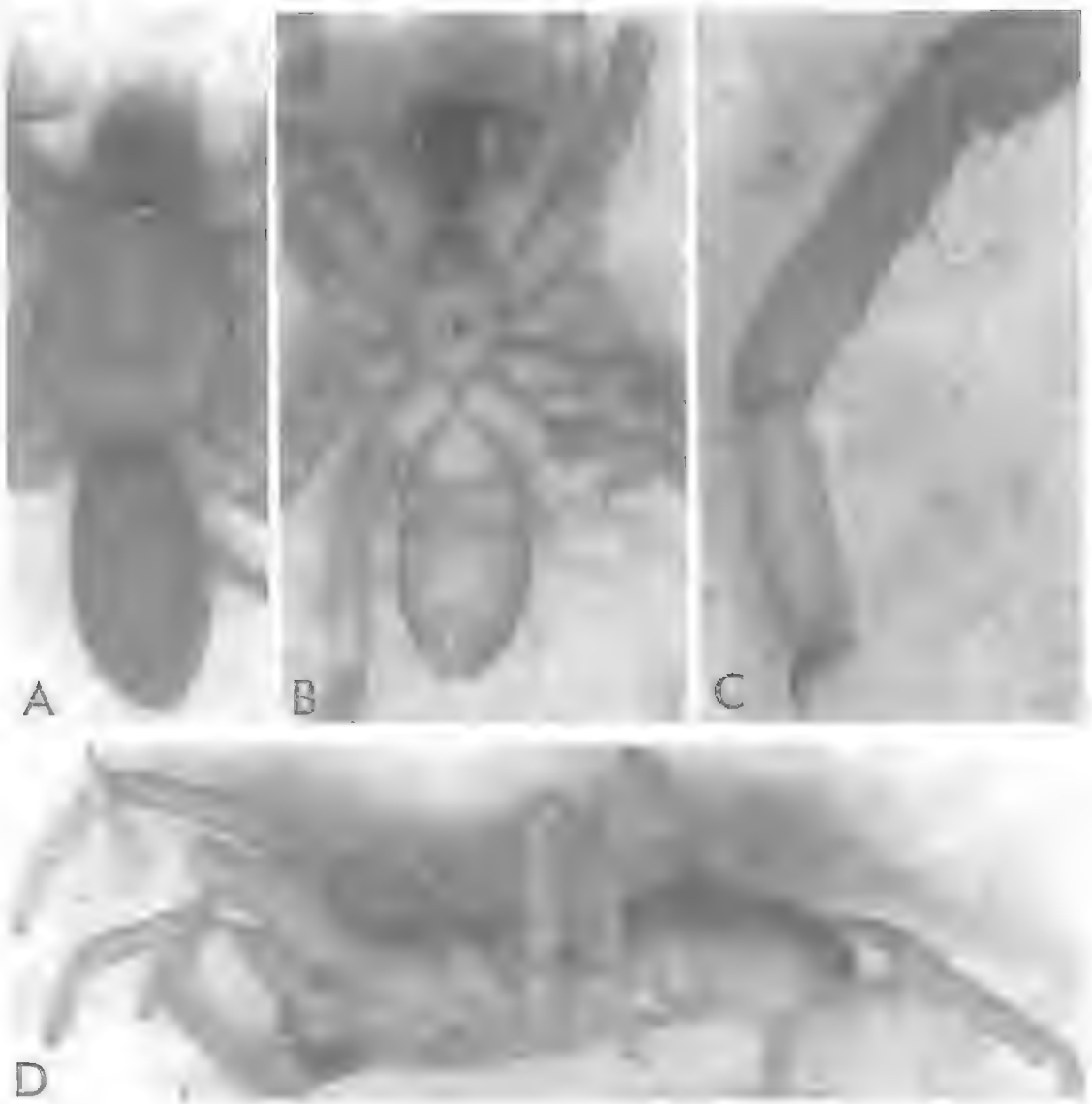



FIG. 5. *Melloina rickwesti* sp. nov., holotype female, micrographs. A, D, carapace, chelicerae, legs and abdomen, dorsal (A) and lateral (D) views. B, chelicerae, sternum, maxillae, labium, legs and abdomen, ventral view. C, leg I, retrolateral view.

*Spermathecae*. Two long undivided lobes.

REMARKS. The differences between the male of *M. gracilis* and female of *M. rickwesti* are greater than that found between male and female conspecific paratropidines in a pending revision of the sister subfamily (pers. obs.). Hence, the difference between the two animals is more than sexual dimorphism.

The tarsal organ of *Melloina* sp. (Raven, 1994: fig. 19A) is that of *M. rickwesti*.

ACKNOWLEDGEMENTS

I am grateful to a number of people. Christine Stocker, Naturhistorisches Museum, Basel, mostly kindly loaned the type of *Melloa gracilis* Schenkel. Rick West, Canada, and Arthur Decae, National Museum of Natural History, Leiden, donated the material of *M. rickwesti*. Line drawings of *M. rickwesti* are by Bronwyn Mitchell. Helen Stark assisted in figure preparation. Along with providing a superbly

productive environment in AMNH during 1983, Norman Platnick commented on the manuscript. This study was partially funded by an Australian Research Council grant to the author.

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# A NEW GENUS AND SPECIES OF ANT-MIMICKING JUMPING SPIDER (ARANEAE: SALTICIDAE) FROM SOUTHEAST QUEENSLAND, WITH NOTES ON ITS BIOLOGY

MICHAEL G. RIX

Rix, M.G. 1999 06 30: A new genus and species of ant-mimicking jumping spider (Araneae: Salticidae) from southeast Queensland, with notes on its biology. *Memoirs of the Queensland Museum* **43**(2): 827-832. Brisbane. ISSN 0079-8835.

A new genus and species, *Judalana lutea*, is described. Cheliceral horns in the male and enlarged spermathecae in the female separate *Judalana* from *Rhombonotus*. ❐ *Salticidae, Judalana, Rhombonotus, Queensland, Australia.*

*Michael G. Rix, 118 Arnold Street, Holland Park 4121, Australia; 4 August 1998.*

Studies on jumping spiders in Queensland have been largely taxonomic, e.g. Davies & Zabka (1989). There are also a number of behavioural studies on N Queensland taxa including *Portia* (see Jackson, 1982), *Myrmarachne 'lupata'* (see Jackson, 1986a), *Mopsus mormon* (see Jackson, 1983), *Euryattus* (see Jackson, 1985a), *Simaetha* (see Jackson, 1985b), *Cosmophasis* (see Jackson, 1986b), *Bavia* (see Jackson, 1986c), *Jacksonoides* (see Jackson, 1988a) and *Tuala* and associated prey (Jackson, 1988b), to name but a few.

During studies on the spiders of SE Queensland, a new ant-mimicking jumping spider resembling the pluridents *Rhombonotus* was discovered on *Acacia* bushes. It is described here.

## METHODS

Descriptions are based on specimens preserved in 75% ethanol. All measurements in millimetres and are taken by camera lucida projection.

## Order ARANEAE
## Family SALTICIDAE
## Group PLURIDENTATI
## **Judalana** gen. nov.

ETYMOLOGY. For my parents, Judy and Alan.

TYPE SPECIES. *Judalana lutea* sp. nov.

DIAGNOSIS. The unique presence of frontal cheliceral horns in the male and enlarged, bulbous spermathecae in the female separate *Judalana* from other related taxa. As in *Rhombonotus*, the posterior lateral eyes (PLE) are on the edge of the carapace and the insemination ducts are simple and uncoiled. Males with two abdominal scuta.

SPECIES INCLUDED. *Judalana lutea* sp. nov.

DESCRIPTION. Small ant-mimicking salticids with bright, yellow-orange abdomen. Cylindrical and slender, these spiders are distinctive pluridents.

COMPARISON. *Judalana* appears to be closely related to the other 4 genera of Australian plurident ant mimics: *Ligonipes*, *Rhombonotus*, *Damoetas* and *Myrmarachne*. The diagnoses of these genera are confused and a revision is needed. *Judalana*, however, differs from the above genera (as defined by Davies & Zabka, 1989) by the posession of enlarged spermathecae in the female and frontal horns on the male chelicerae. An undescribed plurident ant-mimic from near Birdsville, SW Queensland, also has the latter characteristic, albeit modified.

BIOLOGY. Known only from SE Queensland, Australia, in open forest, *Judalana lutea* are slender, attractive and energetic spiders which so far have been found mainly on *Acacia* bushes, especially *Acacia aulococarpa*. The ant *Opisthopsis rufithorax*, which the adult spiders strongly resemble, can also be found on these bushes.

## **Judalana lutea** sp. nov.
## (Figs 1-3)

ETYMOLOGY. Latin *luteus* meaning orange or off-yellow, referring to the distinctive abdominal coloration of this species.

MATERIAL. HOLOTYPE: QMS31518, M, Tarragindi, Brisbane, 27°32'15"S 153°02'30"E, 22 Jun 1996, M. Rix. ALLOTYPE: QMS31519, F, same data. OTHER MATERIAL. QMS41438, 41439, M, F, Mulgowie, 27°44'S, 152°00'E, SE Qld, 25 Mar 1981, M. Grant; QMS41446, F, Kumbarilla, W of Dalby, 27°19'S, 151°00'E, SE Qld, Feb 1978, T. Adams; QMS31523, Redbank Plains, 27°39'S, 152°52'E, SE Qld, 4 May 1997, M, M. Rix; QMS31522, Holland Park, 27°31'S, 153°04'E,

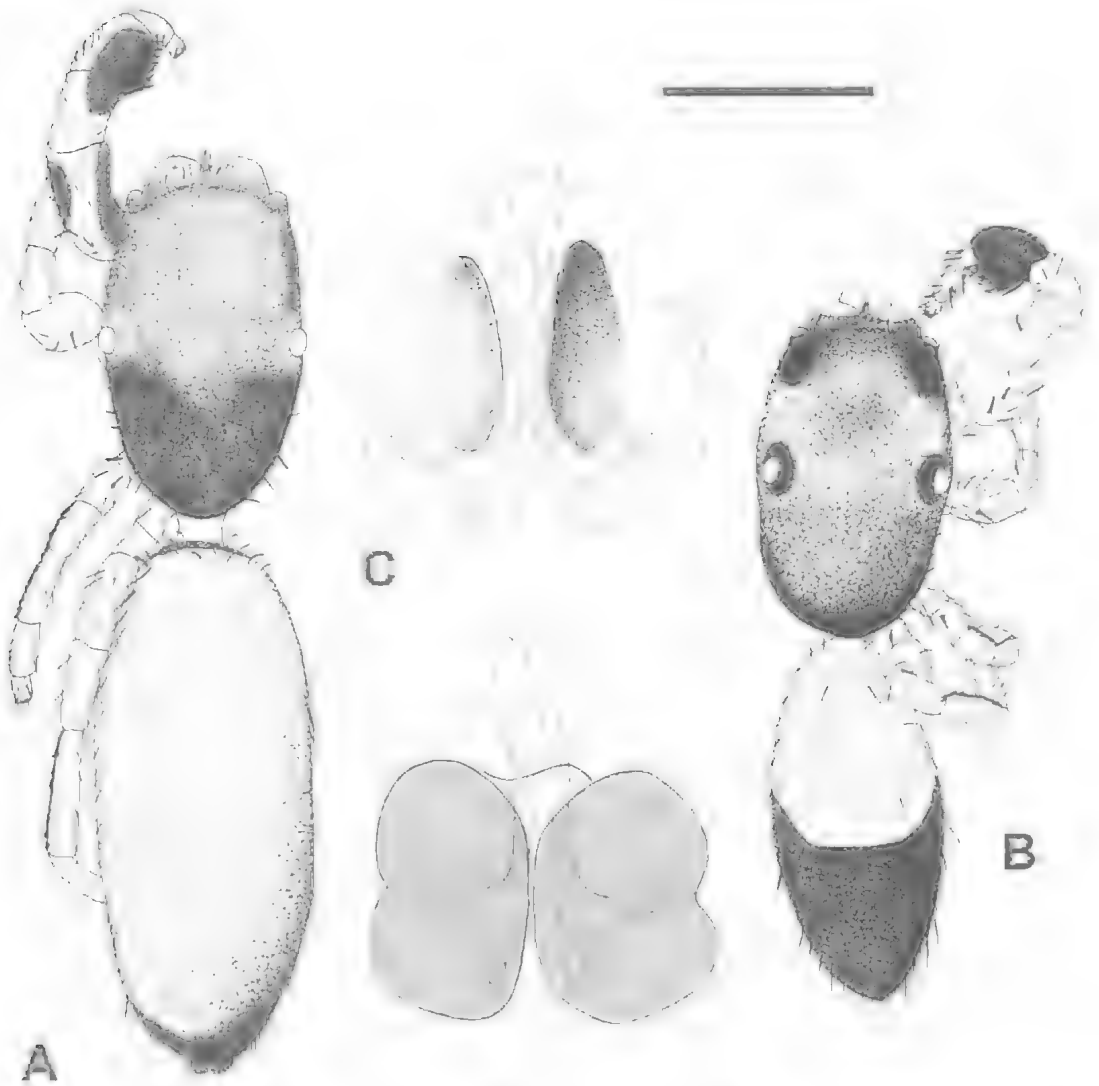



FIG. 1. *Judalana lutea* sp. nov. A, B, habitus. A, allotype female. B, holotype male. C, D, epigynum. C, external; D, internal. Scale bar = 1mm (A,B), 0.26mm (C, D).

SE Qld, 11 May 1997, F, M. Rix; QMS31521, Whites Hill, 27°31'S, 153°05'E, SE Qld, 9 Nov 1997, M, M. Rix; QMS31524, Carina, 27°30'S, 153°06'E, SE Qld, 25 July 1997, F, M. Rix; QMS31520, Mt Coot-tha, 27°29'S, 152°52'E, SE Qld, 4 May 1997, M, M. Rix; QMS43708, Camira, 27°38'S, 152°55'E, SE Qld, 22 Dec 1997, M, K. Walker.

DIAGNOSIS. As for genus.

DESCRIPTION. Holotype male QMS31518. Carapace 1.50 long, 0.90 wide. Abdomen 1.70 long, 0.80 wide. Total length 3.20. Carapace dark orange. All eyes bordered in black. Dorsal abdomen orange anteriorly and black posteriorly; colours centrally divided. Ventral abdomen mottled yellow and black. Carapace with pale hairs laterally. Dorsal row of downward curving setae along top margin of anterior eye row; hairs longer towards the centre. Posterior median eyes (PME) and PLE slightly raised, PLE more so. PLE on edge of carapace. PME closer to anterior eye row than posterior. Abdomen oval, elongated, covered in downy hairs. Leg I incrassate; orange with black tibia armed with brush of flattened black hairs. Two short spines on ventro-prolateral edge of tibia I. Three on

TABLE 1. Palp and leg measurements, holotype male QMS31518.

| | Palp | I | II | III | IV |
|---|---|---|---|---|---|
| Coxae | 0.06 | 0.30 | 0.24 | 0.18 | 0.16 |
| Trochanter | 0.12 | 0.12 | 0.12 | 0.10 | 0.10 |
| Femur | 0.49 | 0.89 | 0.57 | 0.51 | 0.49 |
| Patella | 0.16 | 0.40 | 0.35 | 0.29 | 0.29 |
| Tibia | 0.18 | 0.55 | 0.33 | 0.31 | 0.33 |
| Metatarsus | | 0.37 | 0.33 | 0.41 | 0.31 |

TABLE 2. Palp and leg measurements, allotype female QMS31519.

| | Palp | I | II | III | IV |
|---|---|---|---|---|---|
| Coxae | 0.34 | 0.31 | 0.25 | 0.18 | 0.22 |
| Trochanter | 0.12 | 0.12 | 0.09 | 0.08 | 0.12 |
| Femur | 0.18 | 0.80 | 0.58 | 0.53 | 0.80 |
| Patella | 0.34 | 0.40 | 0.31 | 0.27 | 0.37 |
| Tibia | 0.12 | 0.49 | 0.31 | 0.33 | 0.62 |
| Metatarsus | | 0.28 | 0.31 | 0.39 | 0.46 |

retrolateral side of ventral fringe. Other legs yellow with margin of black hairs along patellae and tibiae III and tibiae IV. Metatarsus I ventrally with 2 pairs of short spines. Chelicerae each with a horn projecting forward, the spurs crossing over slightly at tip and superficially not unlike the mandibles of an ant; 4 teeth on retromargin, 4 fused on promargin. Palp nearly twice as long as wide, with many serrated hairs. Tibial apophysis bent markedly to left when palp is at retrolateral position. Embolus long, circling tegulum, before continuing past tip of cymbium. Tip of embolus overturned with thinner continuation. Abdomen with black, dorsal, posterior, abdominal scutum, curving laterally. Lighter coloured anterior, dorsal, abdominal scutum. (See Table 1 for leg measurements)

Allotype female QMS31519. Carapace 1.67 long, 0.90 wide. Abdomen 2.40 long, 0.98 wide. Total length 4.14 (including pedicel). Carapace black. Dorsal abdomen orange. Ventrally black with orange epigynum. Carapace with pale hairs laterally. Dorsal row of downward curving setae along top margin of anterior eye row; hairs longer toward the centre. PME and PLE slightly raised, PLE more so. PLE on edge of carapace. PME closer to anterior eye row than posterior. Cheliceral dentition differs from that of the male, 3 fused teeth on both pro- and retrolateral margins. Exterior epigynum with oval fossae. Simple, uncoiled insemination ducts internally leading to enlarged, bulbous spermathecae. Fertilisation ducts long and ventrally obvious. Abdomen oval and elongated, covered in downy hairs. Legs I incrassate; tibia armed with thick brush of flattened black hairs. Two short spines on ventroprolateral edge of tibia I. Three on retrolateral side of ventral fringe. Metatarsus I with four short spines. Other legs pale yellow with margin of black hairs along the patellae and tibiae III and tibiae IV. (See Table 2 for leg measurements)

DISTRIBUTION. *J. lutea* is known from several open sclerophyll forests in SE Queensland with areas of *Acacia* scrub. These include localities in the greater Brisbane area (Tarragindi, Holland Park, Mt Coot-tha, Redbank Plains, Whites Hill, Carina, Camira) and, to the west, Mulgowie and Kumbarilla.

BIOLOGY. To date this cryptic species has been found mainly on *Acacia* bushes and occasionally on eucalypts. Leaves have been folded lengthways or at the tip to create a retreat, with the spider usually concealed inside under a sheet of white silk. This species mimics the ant *Opisthopsis rufithorax*; the adults are similar in size and colour, the male being more like the ant than the female. No specimen has been seen to eat ants.

LIFE HISTORY. The egg sac of *J. lutea* is concealed in the folded leaf that the mother prepares. The egg sac is made of flocculent white silk and contains about 11-14 striking orange eggs. A female with her egg sac stayed with it until the eggs hatched, after which she died. Some females bind their brood chambers with separate parallel bars of silk, attached to the edges of the folded leaf. Adult females are often found inside the folded leaves with their brood. Newly hatched juveniles are very similar in appearance to common small black ants found in the forest. This resemblance is, however, short-lived as they attain their bright adult colour after only a few moults. It is unknown if they feed on these ants in the wild. In captivity, they take tiny flies. Males can be found roaming but have also been found with a female in the folded leaves. Males have not been found with a brooding female. One tiny scelionid wasp, probably *Idris* sp. has been found to attack the eggs of *J. lutea*. In early November 1996, an egg sac in captivity taken from the type locality hatched out several of these wasps. Spiderlings also hatched, so in this case the wasps did not parasitise all the eggs. A male of *J. lutea* was also taken from the nest of a mud wasp, *Sceliphron* sp (Sphecidae).

SYMPATRIC SALTICIDS. The site where *J. lutea* was first discovered, Redbank Plains near

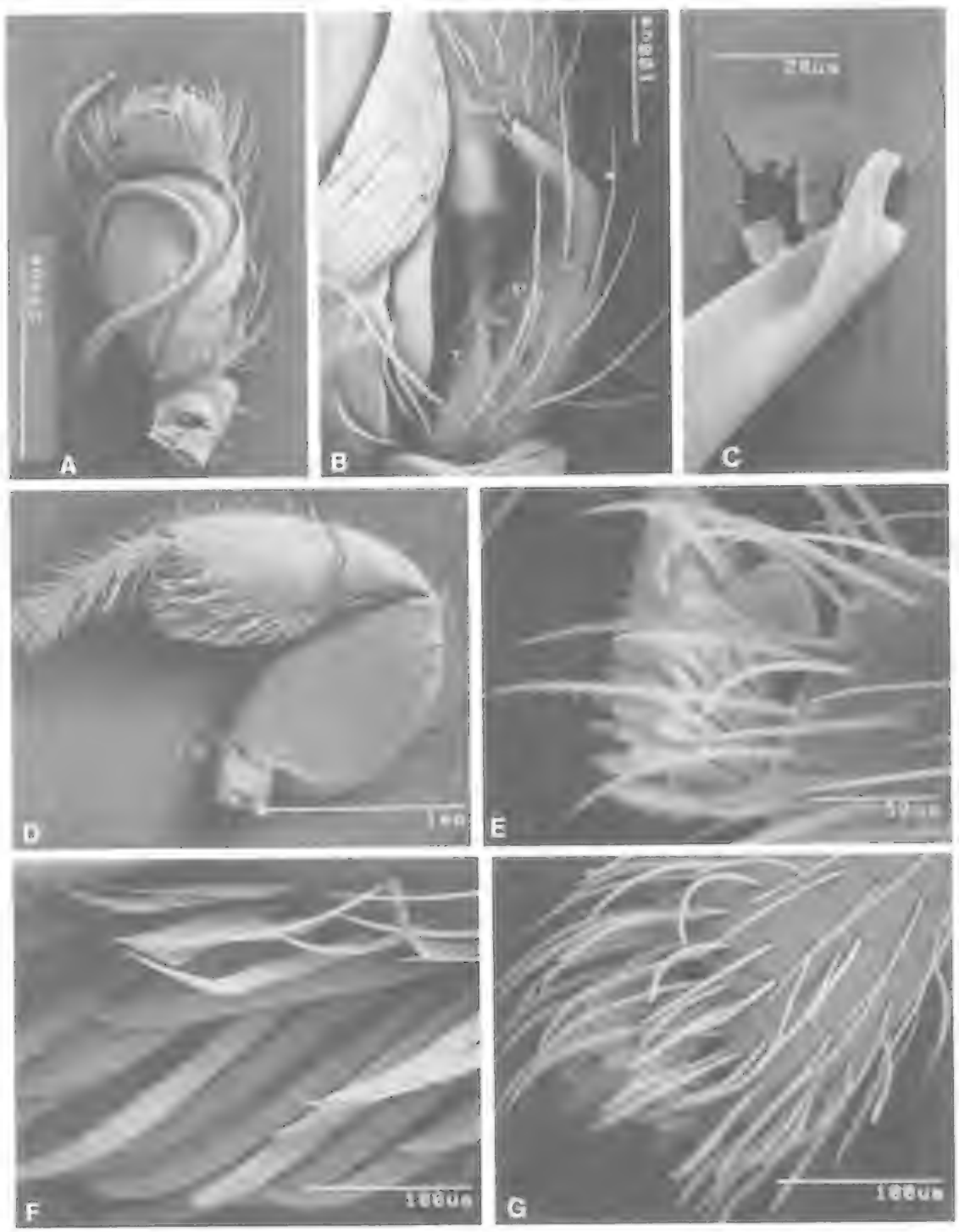



FIG. 2. *Judalana lutea* sp. nov. Scanning electron micrographs. A-C, ventral left palp, male. A, ventral view, bulb; B, tibial apophysis, retrolateral view showing bend; C, tip of embolus, showing curved tip and opening of sperm duct. D-G, leg I, ventral right, male. D, prolateral view; E, G, tip of tarsus & claws; F, tibial hairs.

50%

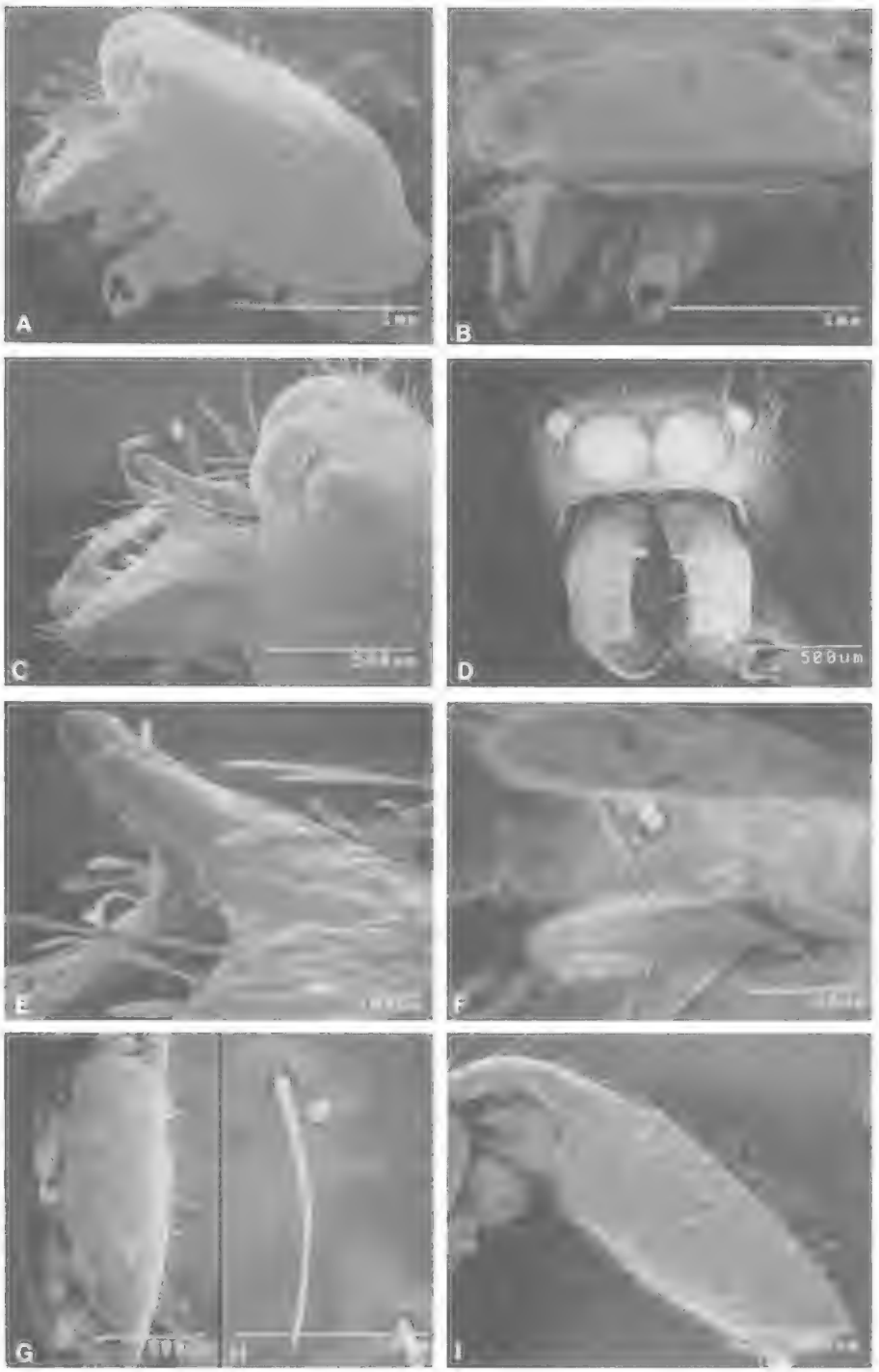



FIG. 3. *Judalana lutea* sp. nov. Scanning electron micrographs. A-C, male, cephalothorax. A, C, dorsolateral view showing spurs; B, lateral view. D, eyes & chelicerae, frontal view. E, cheliceral horns, lateral view. F, cheliceral setae at base of horn, lateral view. G-I, abdomen, male. G, H, posterior dorsal scute; G, ventrolateral view showing curvature; H, enlargement showing transverse ridges & hairs; I, lateral view showing division between anterior and posterior dorsal scuta.

Ipswich, SW of Brisbane, is also home to a species of *Myrmarachne* which mimics the same ant species and has also been found on *Acacia* bushes.

## ACKNOWLEDGEMENTS

To Robert Raven of the Queensland Museum for his invaluable guidance and encouragement in the preparation of this paper, and to Gordon Gordh of the University of Queensland for his assistance in the identification of the ant mentioned in the text. To Valerie Todd Davies for her assistance and to the referees for their detailed and constructive comments. Thanks are also due to Andrew Austin, University of South Australia, for his help in identifying the parasitic wasp and to Chris Burwell, Queensland Museum, for identifying the mudwasp.

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1988b. The biology of *Tuala lepidus*, a jumping spider (Araneae: Salticidae) from Queensland: display and predatory behaviour. New Zealand Journal of Zoology 15(3): 347-364.

# NOTES ON THE CORAL-INHABITING BARNACLES OF THE GREAT BARRIER REEF, AUSTRALIA (CIRRIPEDIA: PYRGOMATIDAE)

ARNOLD ROSS

Ross, A. 1999 06 30: Notes on the coral-inhabiting barnacles of the Great Barrier Reef, Australia (Cirripedia: Pyrgomatidae). *Memoirs of the Queensland Museum* **43**(2): 833-836. Brisbane. ISSN 0079-8835.

Fixation of the type species for *Arossella* Anderson, 1992, *Darwiniella* Anderson, 1992, and *Trevathana* Anderson, 1992 is by monotypy, and for *Wanella* Anderson, 1993 by subsequent designation. *Wanella andersonorum* sp. nov. is proposed for an Australian species from the Great Barrier Reef previously reported as *Wanella elongatum*. *Neotrevathana* gen. nov. is proposed for *Pyrgoma elongatum* Hiro, 1931 from Honshu Island, Japan. ❐ *Wanella andersonorum sp. nov., Neotrevathana n. gen., Pyrgoma elongatum Hiro, type designations, taxonomy.*

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*10 November 1998.*

In the landmark study on the functional morphology of coral-inhabiting barnacles found in Australian waters along the Great Barrier Reef (GBR), Anderson (1992: 329) proposed four new taxa: *Rossia, Darwiniella, Trevathana* and *Newmania.* Unfortunately, the names *Rossia* and *Newmania* were preoccupied and, as replacement names, Anderson (1993: 377) proposed *Arossella* and *Wanella*, respectively. In proposing these, Anderson (1992, 1993) did not follow the general precepts of the 3rd edition of the ICZN (1985). However, three of the taxa fall within 'type by indication' as specified in Article 67b and 68d of the Code, and therefore type designation is type by monotypy. Thus, for *Arossella* the type species is *Pyrgoma projectum* Nillson-Cantell, 1938; for *Darwiniella* the type species is *Pyrgoma conjugatum* Darwin, 1854; and for *Trevathana* the type species is *Pyrgoma dentatum* Darwin, 1854.

When proposing *Newmania* (=*Wanella*), Anderson included two nominal taxa, '*Pyrgoma elongatum*' Hiro, 1931, (='*Wanella elongatum*') and *Pyrgoma milleporae* Darwin, 1854 (=*Wanella milleporae*). Unfortunately, he did not indicate which one was the type species.

The illustrations and description by Anderson (1992: 321, fig. 31) of '*Wanella elongatum*' from the GBR delimit a species that bears little resemblance to that of *Pyrgoma elongatum* described by Hiro (1931: 154; pl. 14, figs 2-2b) from Seto, Honshu I., Japan. As Anderson (1992: 320) unequivocally noted, this Australian species is clearly allied to, but specifically distinct from, the Philippine species *Pyrgoma milleporae* Darwin, 1854, and I concur with this assessment. '*Wanella elongatum*' (sensu Anderson, 1992: 321) represents a new species of *Wanella*, which is described below.

One remaining question is the actual systematic position of *Pyrgoma elongatum* Hiro. The original and subsequent descriptions by Hiro (1931: 154; 1935: 19; 1938: 400) and Galkin (1983: 510) emphasise numerous unique attributes, all of which warrant placement of *P. elongatum* in a new taxon related to, but distinct from, *Trevathana* Anderson, 1992.

## SYSTEMATICS

Suborder Balanomorpha Pilsbry, 1916
Family Pyrgomatidae Gray, 1825
Subfamily Pyrgomatinae Gray, 1825

### **Wanella** Anderson, 1993[1]

*Newmania* Anderson, 1992: 329 (not *Newmania* Swinhoe, 1892, a lepidopteran).
*Wanella* Anderson, 1993: 377 (*nomen novum* for *Newmania*).

[1] [Due to an oversight, I inadvertently omitted designating a type species for one of the genera I proposed in my 1993 paper (Anderson, Zoological Journal of the Linnean Society 108: 377). I would like to correct this herein. Therefore, I designate *Pyrgoma milleporae* Darwin, 1854 to be the type species of *Wanella* Anderson, 1993. - D. T. Anderson, The University of Sydney, Sydney, N.S.W. 2006, Australia.]

DIAGNOSIS (emended). Wall coalescent, non-tubiferous, low conic to essentially flat, ovate to almost circular in outline; orifice small; inner lamina absent; sheath developing on outer lamina, basal margin ovate; opercular plates separate, limbus occludens, or apical occludent ledge lacking; scutum transversely elongate, making up 2/3 or more of operculum, adductor plate lacking, with small rostral tooth, adductor muscle depression divided into rostral and carinal portions; reduced tergum essentially equilateral to subquadrate, discrete spur and spur tooth lacking; basis calcareous, shallow, cup-shaped.

TYPE SPECIES. *Pyrgoma milleporae* Darwin, 1854. Recent, Mindoro Is, Philippine Is, on what is probably *Millepora platyphylla* Hemprich and Ehrenberg, 1834 (not *Millepora complanata* Lamarck, 1816, see remark below).

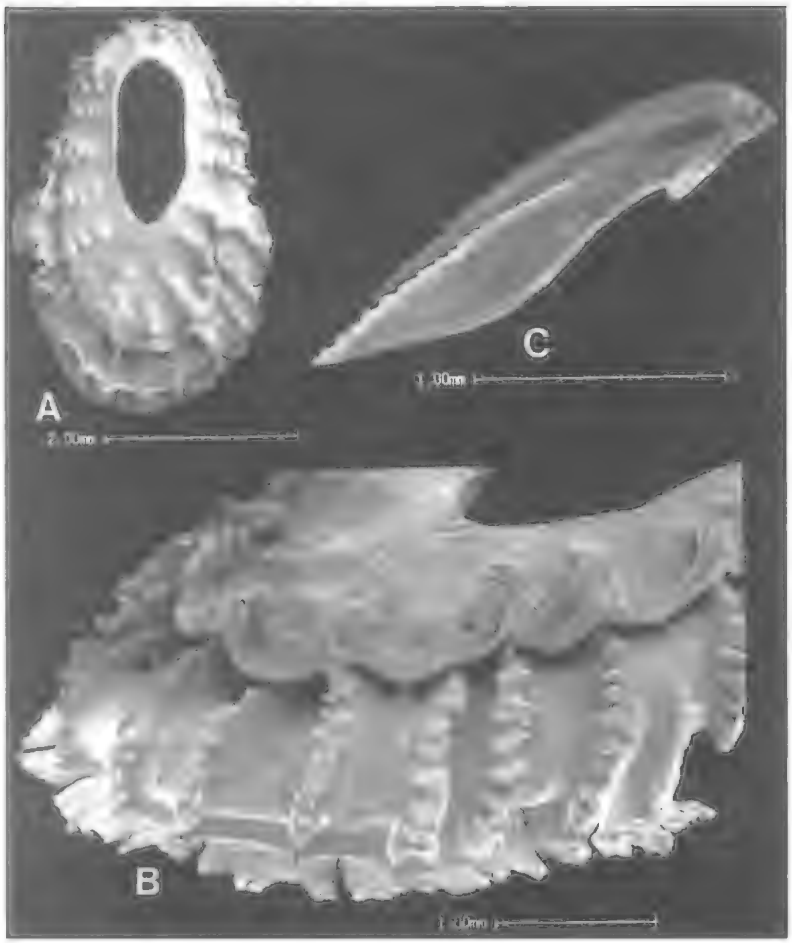



FIG. 1. Scanning electron micrographs of *Neotrevathana elongatum* (Hiro), 1931, Amami O-Shima, Ryukyu Is, approx 28°12'N, 129°30'E, host *Goniastrea aspera* Verrill, 1905, SIO C-9973. A, apical view of wall, rostral end at bottom. B, enlarged view of right rostral end of wall. In this half-grown individual the shallow, narrow pockets below the outer surface of the wall likely contained tissue that inhibits overgrowth by the coral. Regularly spaced black dots along the growth ridges are setal pores that transverse the wall. C, oblique external view of right opercular plate. The simple tergal knob-like projection or spur is visible along the bottom right side of the plate.

REMARKS. As noted above, Anderson assigned two species to *Wanella*, which at the time were included in the genus *Savignium* Leach, 1825 (Ross & Newman, 1973: 159). In the body of the text (Anderson, 1992), the discussion of *milleporae* precedes that of '*elongatum*' (see below). However, in the brief taxonomic section at the end of the paper, their position is reversed (cf. Anderson, 1993). Because there is no clear 'page or line priority' I have asked Prof. Anderson to follow Recommendation 69A of the Code and select the better known, commonly illustrated and more frequently observed (see Boschma, 1948) of the 2 originally included species as the type .

Among the unique features found in both species of *Wanella* is subdivision of the scutal adductor into a 'fast and slow' muscle (Anderson, 1992: 320), as well as a reduced orifice, transversely elongated scuta and reduced terga lacking a spur. Also, the oral cone is large and prominent relative to the reduced thorax and maxillipeds.

According to Boschma (1948: 34), *Millepora complanata* Lamarck, 1816, the type host cited by Darwin (1854: 367), ranges throughout the tropical W Atlantic, and is not known to occur in

the Philippine Is or elsewhere in the W Pacific region. Therefore, the type host is likely that cited above.

**Wanella andersonorum** sp. nov.

*Newmania elongatum:* Anderson, 1992: 320, fig. 31 (not *Pyrgoma elongatum* Hiro, 1931).
*Wanella elongatum:* Anderson, 1993: 377.

ETYMOLOGY. The specific epithet, *andersonorum*, honors Prof. D. T. Anderson and his wife, Joanne T. Anderson, whose collective efforts have expanded greatly our knowledge and understanding of the coral-inhabiting barnacles that abound in Australian waters.

DIAGNOSIS. Scutum with pronounced rostral tooth; adductor ridge long, curvilinear; articular margin curvilinear; tergum essentially irregular in outline, basal margin evenly curved.

DESCRIPTION. Wall low-conic, almost circular in outline; sheath about ½ height of wall, adpressed, lacking lineations in sheath where tergal spur membrane attaches to wall; adductor muscle depression of scutum large, well defined, divided by slight partition; pit for insertion of lateral depressor muscle well separated from basi-tergal angle; articular ridge of scutum extending well over tergum.

TYPE LOCALITY. John Brewer Reef, GBR, off Townsville, N Queensland, Australia, approx. 19°13'S 146°48'E; J. Carleton and A. Mackley coll.; Aug, 1987; on *Montipora* sp.

REMARKS. The tergal margin of the scutum in *P. milleporae* is straight as is the basal margin of the tergum in contrast to the curvilinear margins found in *W. andersonorum*. The lateral depressor muscle pit in *P. milleporae* is at the basi-tergal angle, but in *W. andersonorum* it is well removed rostrally. Also, the tergum approximates an equilateral triangle in *P. milleporae* whereas it is essentially irregular in outline in *W. andersonorum*. The apertural frill, an elaboration of the tergo-scutal flaps, which appears to inhibit overgrowth by the coral (Anderson, 1992: 292) is brown with a white margin in *P. milleporae*, whereas in *W. andersonorum*, it has '... a white rim, a black wall and distinctive brown-pigmented band in contact with the encroaching coral' (Anderson, 1992: 321), features that further serve to distinguish these two species.

The specimens upon which I base this new species were not accessioned by any institution, and thus are not available. Therefore, in accordance with Article 74(c) of the Code, I designate the syntype specimen represented by figure 31c of Anderson (1992: 321) as the lectotype.

**Neotrevathana** gen. nov.

TYPE SPECIES. *Pyrgoma elongatum* Hiro, 1931; Recent, Seto, Honshu I., Japan, 32°58'N 129°39'E; on *Madrepora* sp.

ETYMOLOGY. From Greek, *neo-*, new, and *-Trevathana*, suggesting its relationship and derived phylogenetic position. Gender, neuter.

DIAGNOSIS. Shell coalescent, non-tubiferous, essentially flat, elongate-oval in outline; surface ornamented with widely spaced, low, radiating ridges; orifice large, elongate oval; sheath adpressed, basal margin ovate and saddle-shaped, covering 1/2 or more height of wall; opercular plates coalescent; limbus occludens moderately broad, scutal portion of valve about four times greater than tergal portion; tergal spur reduced or obsolescent; basis calcareous.

REMARKS. *Neotrevathana* differs from *Trevathana* in having broad, low ridges on the shell surface, coalescent opercular plates, a broad occludent ledge (Fig. 1), and by lacking a depression for insertion of the lateral depressor muscle. The tergal spur in *Neotrevathana* is reduced to a knob-like projection, whereas the tergal tooth in *Trevathana* appears to be an elaboration of the tergal spur.

There is no listing for specimens of *Pyrgoma elongatum* Hiro in the cataloge of types in the museum at the Seto Marine Biological Laboratory, Japan (Harada, 1991). According to Harada (in litt., 1994) the type of *P. elongatum* is '... not in the museum and its whereabouts are not known'. A neotype (see Article 75(a) of the Code) should be designated, but the coral fauna in the region of the Seto Marine Biological Laboratory has been seriously affected by pollution and the species may no longer be present there or elsewhere on Honshu I. (Asami & Yamaguchi, 1997: 14), although it is known to occur farther south in the Ryukyu Is (material illustrated in Fig. 1), Hong Kong, Timor Sea and Heron I., Australia (Foster, 1982: 225; Galkin, 1983: 510).

ACKNOWLEDGEMENTS

For assistance and other courtesies I thank D.T. Anderson, University of Sydney, Australia; Penny Berents, Australian Museum, Sydney;

William A. Newman, Scripps Institution of Oceanography, California; Robert J. Van Syoc, California Academy of Sciences, San Francisco; Eiji Harada, Seto Marine Biological Laboratory, Japan, and Kiyotaka Asami, Chiba University, Japan. The comments of two anonymous reviewers is gratefully appreciated. A contribution of the Scripps Institution of Oceanography, new series.

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# PARASITES FROM EAST-COAST AUSTRALIAN BILLFISH

PETER SPEARE

Speare, P. 1999 06 30: Parasites from east-coast Australian billfish. *Memoirs of the Queensland Museum* **43**(2): 837-848. Brisbane. ISSN 0079-8835.

Fifty-two sailfish, *Istiophorus platypterus*, and 63 black marlin, *Makaira indica*, were examined for parasites between 1987 and 1989. Sailfish were collected from 4 locations along the Queensland coast between Cape Moreton in the south and Dunk Island in the north. Black marlin were sampled from a similar range, but extending further north to Lizard Island where large fish, in excess of 450kg, were available. Thirty-one parasite species were identified from sailfish (22 new records) and 28 from black marlin (20 new records). Twenty-four species were shared by sailfish and black marlin. Parasites were also collected from 1 blue marlin, *Makaira mazara*, and 3 striped marlin, *Tetrapterus audax*, taken off Cape Moreton. Ten species of parasites were identified from the blue marlin (6 new records) and 5 from striped marlin (2 new records). Gut analysis revealed a more diverse diet for the sailfish which was reflected in their parasite fauna. ❐ *Istiophorus, Makaira, parasites, Queensland, Australia.*

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Records of parasites from billfishes have usually come from more general surveys of fishes by parasitologists focusing on specific taxa. Prior to this study, 19 species of parasites had been recorded from Pacific sailfish, *Istiophorus platypterus*, and 13 from black marlin, *Makaira indica*.

This report presents the results of an intensive survey of the parasite fauna of sailfish and black marlin along the coast of Queensland, NE Australia. Numerical analyses of the parasites as biological tags were documented in Speare (1994, 1995). This report focuses on ecological notes on these parasites, distributions of parasites on the hosts, and some pathology. Possible sources of infection are discussed based on knowledge of the feeding habits of hosts.

## METHODS

All fish were obtained from recreational fishing activities. Fish were collected between Lizard I., in the northern Great Barrier Reef, to Cape Moreton, off Brisbane between 1987 and 1989. Additionally, one striped marlin, *Tetrapterus audax*, and 3 blue marlin, *Makaira mazara*, were obtained from Cape Moreton waters.

Fish were dissected as described in Speare (1994). Several parasites could be identified from remnants remaining after their death. In these instances, live and dead specimens were distinguished. Didymozoids which were present as immature and mature cysts were enumerated from a subsample of fish. Two parasite species were prevalent on the gill filaments; counts were made from each hemibranch of several fish with sufficient numbers of the parasites to supply distributional information. Where food items were readily identifiable, their prevalence and numerical abundance were recorded. Specimens were stored in 10% buffered neutral formalin or 70% ethanol.

## RESULTS

A total of 35 parasite species were recorded from 52 sailfish (31 species) and 63 black marlin (28 species) (Table 1) [these figures are revised from those published in Speare (1994, 1995) but do not impact on these earlier publications]. Twenty-four species were common to both sailfish and black marlin. There was no significant correlation between total parasite numbers and fish size but, among sailfish the larger infections occurred among the heavier fish, whereas the small and immature black marlin included fish more heavily parasitised than any of the large adults (Fig. 1). There was little difference in the distributions of the major taxa between the 2 hosts with the exception of substantially more cestodes in sailfish (Fig. 2).

ACANTHOCEPHALA. One specimen of *Rhadinorhynchus pristis* was collected from the intestine of a sailfish at Cape Bowling Green in 1987 (Table 1). This species had not been recorded prior to this study from Pacific sailfish or black marlin, but is recorded from *Istiophorus albicans*, the Atlantic sailfish, in the Gulf of Mexico (Luhe, 1911).

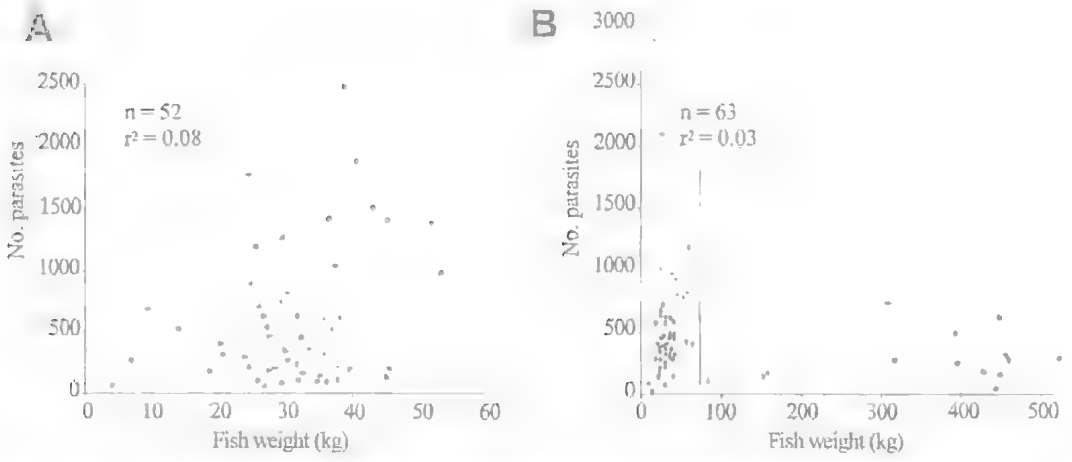



FIG. 4. Relationship between fish weight and total number of parasites for sailfish (A) and black marlin (B). Vertical line in B indicates the transition between immature and mature males which coincides with migration from nearshore shallow coastal to offshore oceanic waters.

CESTODA. *Bothriocephalus manubriformis* is very widespread and host specificity presently extends to 8 of the 12 species of billfish (Xiphiidae and Istiophoridae). All species of trypanorhynchs had not been recorded in these hosts prior to this study. *Callitetrarhynchus gracilis*, *Floriceps minacanthus*, *Otobothrium dipsacum* and *Pterobothrium heterocanthum* were collected from black marlin and sailfish and *Otobothrium* sp. and *Nybelinia* sp. occurred only in sailfish.

Trypanorhynchs were generally of low intensity except *Otobothrium* sp. which had a mean intensity of 150 per sailfish in the Whitsundays (Table 2). The pyloric caecum was the preferred site for this parasite, which was particularly abundant in fish which had fed on pelagic triggerfish, *Balistoides* sp.

COPEPODA. *Caligus* sp. was restricted to the gill filaments of all fish except Lizard I. black marlin (Table 2). They were most abundant among sailfish from Cape Moreton where all fish were infected at an average of 138.8 (n = 19). The number of *Caligus* sp. on the gills of sailfish (n=8) and black marlin (n=6) was recorded for each hemibranch. This copepod displayed a preference for aggregating on hemibranchs 5 to 8 with the majority aggregated on a pair of opposing hemibranchs, especially towards the ventral anterior aspect of a hemibranch (Fig. 3). Localised erosion of the epithelium was evident where this parasite aggregated.

*Gloiopotes huttoni* was least prevalent on adult black marlin from Lizard I. but could otherwise be considered as ubiquitous. The pennellid, *Pennella instructa*, was predominantly buried in the muscle dorsally. It was more prevalent among sailfish than black marlin and especially fish from Cape Moreton. Infrequently, *P. instructa* passed through the peritoneum and into an ovary and effectively blocked the lumen.

Counts of *P. instructa* differentiated live parasites as well as remnants of the cephalothorax surrounded by scar tissue. One percent of all pennellids in black marlin were remnants, whereas this figure was 65% in sailfish. Undeveloped female *P. instructa* occurred only on black marlin from Lizard I. in 1988 (spring). Where several pennellids were present on a fish, there was a tendency to aggregate. Information on group size was collected from 4 sailfish and 9 black marlin (Fig. 4). The most frequent grouping was 1 and the median group size was 2. Among fish with heavy infections of *P. instructa*, up to 24 copepods were closely attached. In the instance of a black marlin from Dunk I., where 132 pennellids were attached in groups of 3 to 24, severe localised muscle necrosis was observed. This fish, which weighed 38kg, had a lowerjaw fork length of a 50kg fish, indicating considerable loss of condition (Fig. 5).

One specimen of *Philichthys xiphiae* (female) was collected from a depression in the right frontal bone of a sailfish from Cape Moreton in 1989. It had previously been recorded from broadbill, *Xiphias gladius*, with the latest record in 1913 (Scott & Scott, 1913). If Thomson's

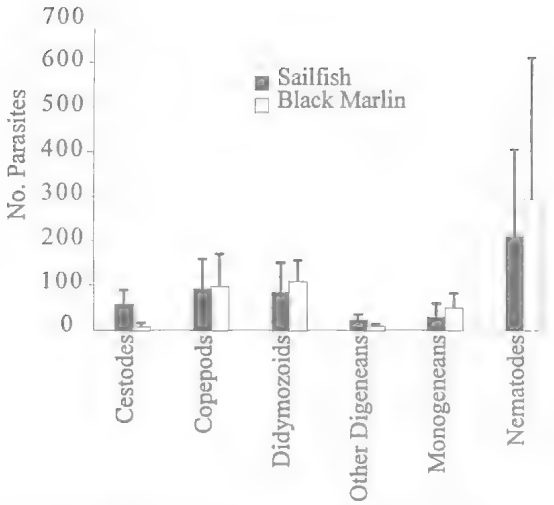



FIG. 2. Average number of parasites (+1SD) of the major taxa collected from sailfish (n = 52) and black marlin (n = 63).

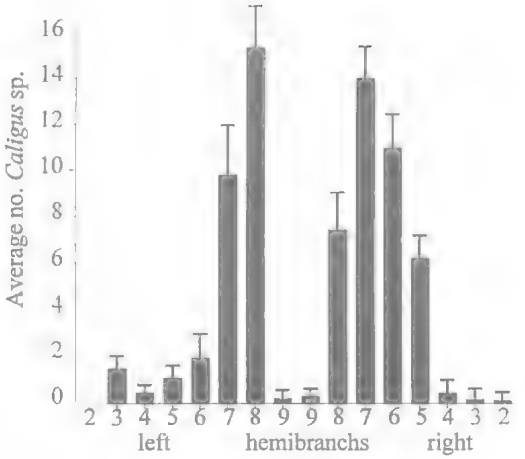



FIG. 3. Average distribution of *Caligus* sp. on the gills of sailfish (n = 8) and black marlin (n = 6). This copepod selected hemibranchs 5 to 8 and was usually aggregated on the anterio-ventral section of the gills. The numerals on the X axis indicate hemibranchs from left to right side.

(1889) record from New Zealand is discounted (as argued by Kabata, 1979), then it is also the first record from the Pacific Ocean.

DIGENEA. Twelve species of digeneans were recorded in black marlin and 13 in sailfish. With the exception of *Cardicola* sp., all digeneans recorded in black marlin also occurred in sailfish. Didymozoids were the most diverse group of parasites collected from these hosts (10 species). Two metacercaria, recognised as *Neotorticaecum* (Kurochkin and Nikolaeva, 1978) and *Torticaecum* (Yamaguti, 1971), were collected from the stomachs of sailfish.

*Glomeritrema subcuticola* was distributed almost exclusively on the head and inferior to the pseudobranchs where they were often densely aggregated. On the head, they overlaid the frontal and sphenotic bones. Both live and dead parasites were distinguished for 27 black marlin. While total counts were only slightly correlated with fish weight ($r^2$ = 0.16), the proportion of live cysts was highly negatively correlated ($r^2$ = -0.82) with fish weight (Fig. 6). Large fish from Lizard I. had proportionately fewer viable cysts than juvenile black marlin from nearshore waters although, on average, they had more cysts. Extensive ulceration, attributed to *G. subcuticola*, was observed below the pseudobranchs of 2 juvenile black marlin taken over the summer months off Cape Moreton (Fig. 7).

*Makairatrema musculicola* was more prevalent and with higher intensities of infection in sailfish than black marlin. Only black marlin from Cape Bowling Green were infected (9.1%) whereas sailfish from Cape Bowling Green and Cape Moreton had infections ranging up to 67 parasites (Table 2). This parasite was very discrete in its distribution on the host; subdermal cysts were exclusive to the dorsal body immediately inferior to the first dorsal fin. All cysts were well developed or spent and with a patent external pore suggesting reproductive activity (Fig. 8). *M. musculicola* had only previously been recorded from black marlin in Hawaii where it was encysted in the ventral abdominal muscle (Yamaguti, 1970), a site from which only *Neodidymozoon macrostoma* was taken in this study.

*Neodidymozoon macrostoma* was encapsulated towards the anterior half of the fish and especially about the lateral line/red muscle, fin membranes and the buccal cavity. This parasite, when mature, could be detected as a raised lump under the skin or through locating a small pore on the skin of the fish. Data were collected on the occurrence of immature (no eggs), mature and dead *N. macrostoma* from 39 black marlin (Fig. 9). Immature cysts occurred in fish from Cairns, Dunk I., Cape Bowling Green and Cape Moreton, at up to 25% of infection levels. The majority of parasites were alive at these localities whereas at Lizard I., approximately 50% were dead and there were no immature cysts.

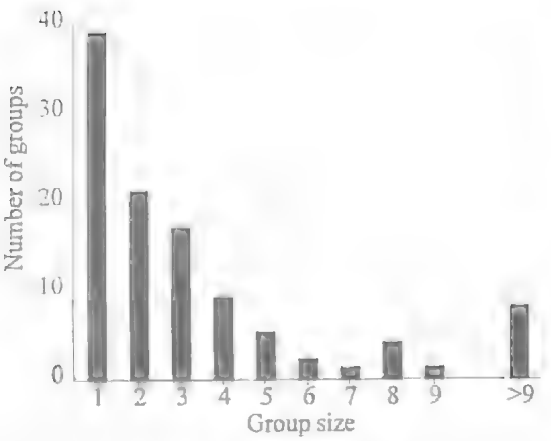



FIG. 4. Frequencies of group size of *Pennella instructa* on sailfish (n = 4) and black marlin (n = 9) from Queensland coastal waters. Median group size was 2 copepods.

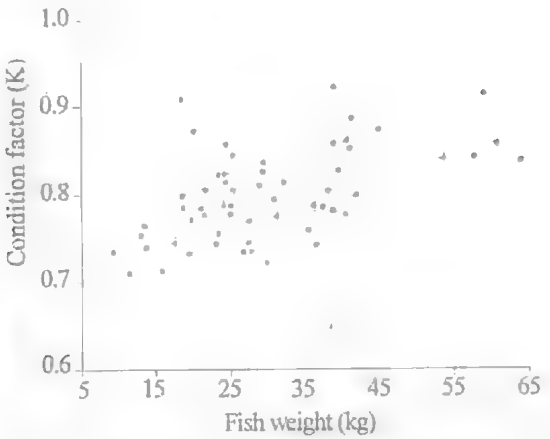



FIG. 5. Condition factor (K) for small, predominantly juvenile, black marlin (n = 59) from nearshore Queensland coastal waters. A fish ( ) with a heavy infestation of *Pennella instructa* had a lower K value than all other fish. $K = 100 \times Wt/LJFL^3$ (units in gm and cm).

*Metadidymozoon branchiale* was, on occasion, abundant on sailfish. Over 1000 pairs of this parasite were collected from the gills of a sailfish at Cape Moreton. It was not recorded among Lizard I. black marlin. This parasite, unlike *Caligus* sp., did not display a marked preference for specific hemibranchs.

*Neodidymozooides microstoma* was encapsulated in the pyloric caeca of 2 sailfish. All parasites were dead in the sailfish from Cape Bowling Green whereas they were alive in the Cape Moreton fish and measured between 15 and 50mm in diameter. Yamaguti (1970) recorded this didymozoid from striped marlin, *Tetrapterus audax*, black marlin and shortbilled spearfish, *T. angustirostris*, in Hawaii where it was parasitic on the serosa of the pyloric caecum. It occurred in a blue marlin, *Makaira mazara*, taken at Cape Moreton in this study (Table 1).

*Cardicola grandis* parasitised the heart and ventral aorta of sailfish and black marlin from each area. *Cardicola* sp. was collected from a black marlin at Lizard I. and a blue marlin at Cape Moreton. The afferent branchial arteries were isolated and dissected out of several fish but, few *C. grandis* were collected from these arteries suggesting that this parasite is specific to the ventricle and ventral aorta. Only 1 specimen of *Hirudinella marina* was collected from a sailfish whereas 73% of black marlin from Lizard I. were infected. Thus, it was essentially absent from sailfish and juvenile black marlin in the shallow nearshore areas.

MONOGENEA. Four species of monogenea were parasitic on black marlin. *Capsaloides cristatus* was on the gills of 1 black marlin from Cape Moreton. *Capsaloides istiophori* was collected from the gill filaments of both sailfish and black marlin (Table 1). It was particularly prevalent and abundant among sailfish from Cape Moreton and was not recorded, as was *C. tetrapteri*, on any black marlin north of Cape Bowling Green (Table 2).

*Tristomella pricei* was ubiquitous, occurring on all black marlin and between 33% and 90% of sailfish on an area basis. While it was predominant on the skin of sailfish and juvenile black marlin, it was restricted to the buccal cavity of mature black marlin from Lizard I. (Fig. 10). Where it aggregated on the fish, there was extensive dermal erosion and *Gloiopotes huttoni* was often similarly aggregated at these sites.

NEMATODA. Four species of adult nematodes were identified from the stomach and intestinal lumen of black marlin (3 species) and sailfish (2 species). These parasites were identified by Bruce and Cannon (1989) and no attempt was made to enumerate their individual distributions due to the intensive microscopic work required to do so. Larvae were also in the stomach mucosa (probably *Contracaecum* sp.) and encapsulated in the intestinal serosa. Billfish have the capacity to fully evert the stomach as there are no mesenteries directly attached to it. This behaviour is

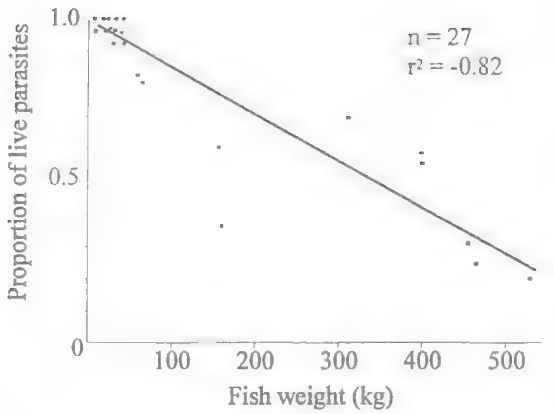



FIG. 6. The relationship between the proportion of live cysts of *Glomeritrema subcuticola* and fish weight was highly negatively correlated in black marlin indicating a more recent exposure to infection among the small juvenile fish in nearshore coastal waters.

readily encountered during sportfishing and may be a stress response but, additionally, may serve to evacuate bones and perhaps rid the animal of parasites of the lumen. A juvenile black marlin from Cape Bowling Green had suffered some form of trauma resulting in the stomach becoming attached to the ventral body wall. This effectively precluded eversion of the stomach which contained 854 nematodes whereas the average infection for black marlin was 33.2 (± 130.8).

BLUE MARLIN AND STRIPED MARLIN. Bruce & Cannon (1989) described 2 new species of nematodes in striped marlin from material collected in this study. Also, an undescribed sanguinicolid, *Cardicola* sp. was parasitic in the heart and ventral aorta of 2 of the 3 blue marlin dissected. All other parasites collected from these fish were also in sailfish and black marlin (Table 1).

FEEDING ECOLOGY. Thirty-four sailfish were examined for recognisable food items in the stomach. Pilchards, *Amblygaster sirm*, and longtoms, *Tylosurus* sp., were present in 57% of stomachs. Pelagic triggerfish, *Balistoides* sp., and toadfish, (Tetraodontidae), were numerically abundant but occurred only in fish from the Whitsundays and Cape Moreton, respectively. Among the 41 juvenile black marlin from the nearshore fishing grounds, pilchards, *Amblygaster sirm*, and herrings, *Sardinella gibbosa*, accounted for 93% of all food items and occurred in 85% of stomachs. *Sarda* sp. were only in Cape Moreton fish stomachs. Pilchards were, by far, the most abundant and prevalent prey of marlin from nearshore coastal waters (Table 3). Lizard I. black marlin stomachs were invariably empty which, in some instances, was clearly due to evacuation of the stomach while the fish was being caught. Remnants of other billfishes were taken from the stomach wall of 4 of the 13 Lizard I. fish.

## DISCUSSION

The parasites recorded in this study significantly increase the number of parasites recorded from sailfish and black marlin. The parasite fauna of sailfish, prior to this study, was much better known than that of black marlin.

Larval trypanorhynchs quite often parasitise a wide range of hosts and it is not surprising to document additional hosts for the species collected in this study. *Callitetrarhynchus gracilis* is reported from approximately 20 fishes and *Floriceps minacanthus* from at least 6 fishes. Evidence suggests that there is little host specificity at the level of the second intermediate host. For example, *F. minacanthus* has previously been recorded from coral trout, *Plectropomus leopardus*, and flathead, *Platycephalus laevigatus*, as well as barracuda, *Sphyraena novaehollandiae*.

The large numbers of *Otobothrium* sp. collected from the pyloric caeca of sailfish from the Whitsundays may be related to feeding on *Balistoides* sp. There were many blastocysts in the stomachs of these fish although, it is not known whether the source is the trigger fish itself or its food which would include copepods.

The three frequently recorded parasitic copepods were widely distributed among sailfish and black marlin. The most conspicuous feature of these distributions was the absence of *Caligus* sp. from Lizard I. black marlin. Additionally, this parasite was unevenly distributed on the gill filaments of the host. Benz & Dupre (1987) found that the abundance of *Kroyeria carchariaeglauci* increased with the surface area of the gills of the blue shark, *Prionace glauca*, which may have simply been due to an increase in the availability of suitable habitat. The distribution of parasites on the gills is generally believed to be related to respiratory water flow (e.g. Fryer, 1968; Hanek & Fernando, 1978) but, distribution varies among copepod species which suggests additional factors are involved (see Rohde, 1979). The absence of *Caligus* sp. from Lizard I. fish may be related to the availability of suitable habitat. As black marlin age, the gill lamellae become increasingly calcified which may render the gills unsuitable



FIG. 7. Photomicrograph of *Glomeritrema subcuticola* and overlying necrotic tissue presumably as a consequence of the capsule rupturing. d = dermis, n = necrotic tissue, p = parasite. Scale bar = 1mm.

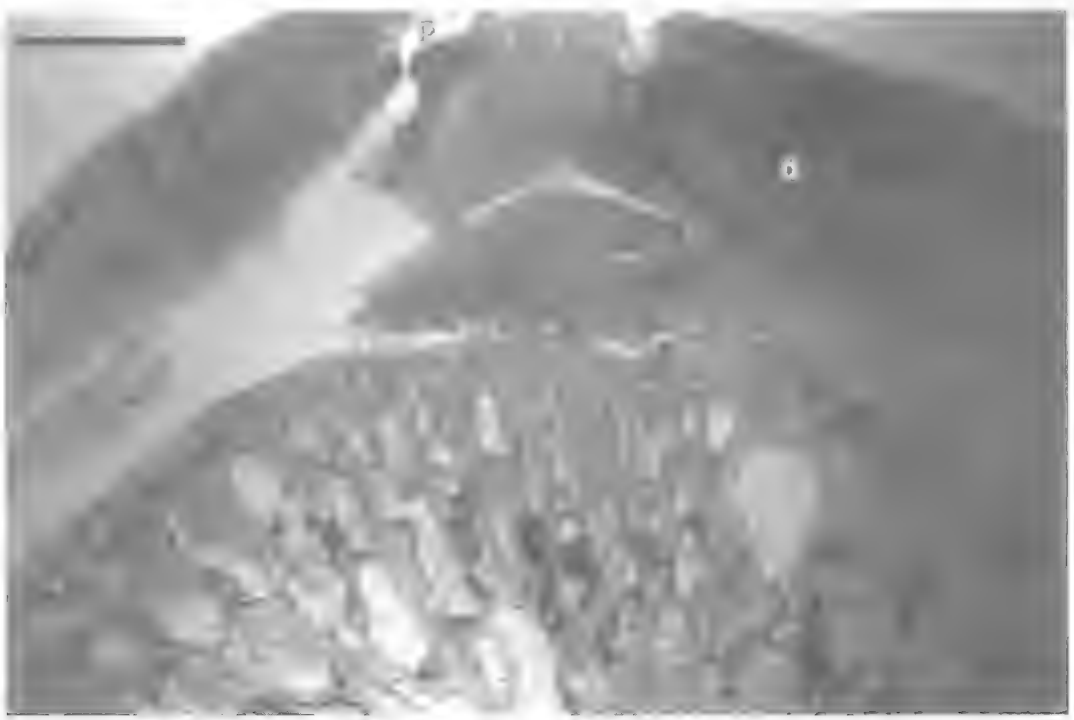


FIG. 8. Cyst of the didymozoid, *Makairatrema musculicola*, displaying a conspicuous external pore. d = dermis, o = ovary, p = pore. Scale bar = 2mm.

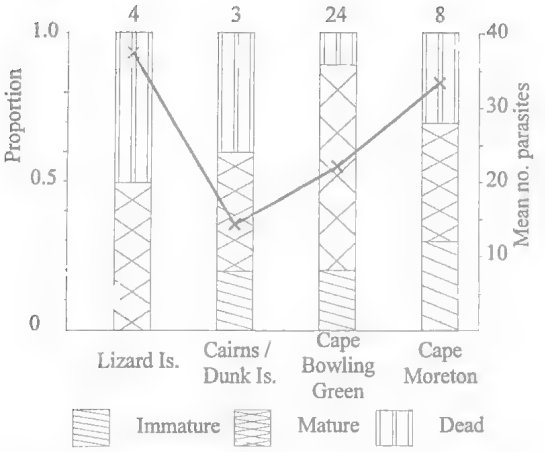



FIG. 9. Proportion of immature, mature and dead cysts of *Neodidymozoon macrostoma* on black marlin indicated continued exposure to infection among juveniles in nearshore waters and lack of recent reinfection among mature offshore fish (Lizard I.). Mean number of parasites per infected fish is shown on the right hand axis and the numbers of marlin from which this information was collected is shown above the bars.

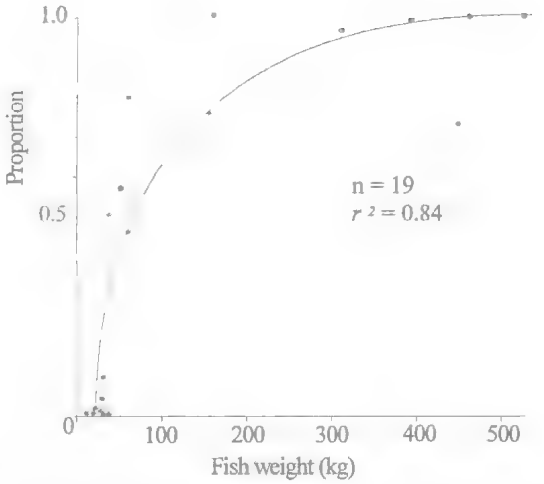



FIG. 10. Proportion of the total infection of *Tristomella pricei* inhabiting the buccal cavity of black marlin. There was a dramatic shift in the predominant site of infection with the size of the fish.

for attachment and feeding. Such ontogenetic changes may also explain the absence of *Metadidymozoon branchiale* from the gills of these large fish, whereas up to 70% of juveniles were infected. In contrast, *Tristomella pricei* numbers were positively correlated with the size of black marlin ($r^2 = 0.24$). Also, this parasite was predominant in the mouth of the large fish whereas its preference was the external body surface of juvenile fish. This aggregation in the buccal cavity of large marlin may represent a move to a more favourable habitat than is available with the tougher and thicker skin found on the adult.

Distributions of *T. pricei* and *Gloiopotes huttoni* on black marlin were not correlated ($r^2 = 0.05$) but there was evidence of co-occurrence on sailfish ($r^2 = 0.23$). While data were not collected, it was visually evident that a densely aggregated group of *T. pricei* often included a similar aggregation of *G. huttoni* on sailfish. *T. pricei* feeding activities in these observations were responsible for severe erosion of the dermis and this activity may present an opportunity of enhanced feeding for *G. huttoni*.

Pennellids have been reported as pathogenic even at very low levels of infection (Kabata, 1958). Where *P. instructa* had penetrated the ovaries of sailfish, histology did not reveal a reduction in reproductive ability. Alternately, the heavily parasitised black marlin from Dunk I. had shed approximately 25% of its body weight indicating a substantial impact from this infection.

The far greater incidence of dead parasites embedded in the flesh of sailfish, as opposed to black marlin, may be related to the respective ages of these fishes. A sailfish of 30kg may be 5 or 6 years old whereas a black marlin of this size would be less than 3 years of age. Consequently, among fish of comparable size, sailfish have been exposed to infection for considerably longer periods which are well beyond the life-span of the parasite.

*Philichthys xiphiae* is a particularly rare parasite. It is the only representative of a genus belonging to a small family (approximately 38 species) of endoparasitic copepods. Kabata (1979) documents it as a parasite of the ducts and sinuses in the frontal bones of broadbill, *Xiphias gladius*. Its recorded distribution in this host is restricted to the Kattegat (Bergsoe, 1864), the western Mediterranean (Brian, 1905), the Adriatic Sea (Valle, 1890), the Belgian coast (Beneden, 1861), Martha's Vineyard (Wilson, 1932) and England (Scott & Scott, 1913). The present record confirms this parasite's high degree of site specificity and the probability, as with other species of copepod, of its occurrence in other species of billfish.

Didymozoids were the best represented family of parasites collected from sailfish and black marlin. Didymozoids have a tropical and

subtropical distribution (Yamaguti, 1970; Hewitt & Hine, 1972; Margolis & Arthur, 1979). They are particularly prevalent among tuna. For example, 37 species are recorded from yellowfin tuna, *Thunnus albacares*, 33 from skipjack, *Katsuwonus pelamis*, 25 from bigeye tuna, *Thunnus obesus*, and 16 from albacore, *Thunnus alalunga* (see Nikolaeva, 1985). Among the istiophorids, 6 species of didymozoids are recorded from Atlantic blue marlin, *Makaira nigricans*, 4 from striped marlin, *Tetrapterus audax*, and 2 from short-billed spearfish, *T. angustirostris*. These figures are still low in comparison with tunas and probably reflect a lack of widespread geographical examination of these fishes' parasite fauna and inspection of tissues where didymozoids typically encapsulate.

Lester (1980) considered that the release of eggs through ulceration of the overlying dermal tissue may be widespread among didymozoids. The ulceration associated with *Glomeritrema subcuticola* was observed in juvenile black marlin and was, therefore, not associated with host spawning as suggested for *Neometadidymozoon helicis*. Adult fish off Lizard I. only had infections of mature, gravid or dead parasites in the spring spawning months. The occurrence of a small 'pin prick' hole above gravid *Neodidymozoon macrostoma* and a more obvious patent external pore associated with gravid *Makairatrema musculicola* suggest a possible mechanism for the release of eggs in these didymozoids.

An hypothesis of southerly migration of juvenile black marlin is supported by an increase in the average size of fish with latitude, movements of tagged fish and a seasonal shift in the availability of fish to recreational game fishers (Pepperell, 1989). Parasitological data (Speare, 1994) suggests a common stock of juvenile black marlin on the east coast. The average intensity of infection and incidence of immature *Neodidymozoon macrostoma* on juvenile black marlin appeared to increase with latitude (refer to Fig. 9) and, coupled with similar prevalence on each fishing

TABLE 1. Parasite species collected from billfishes in Queensland coastal waters. Sa = sailfish, Bk = black marlin, Bl = blue marlin, St = Striped marlin. * new host record for black marlin, † new host record for sailfish, # new host record for blue marlin, ‡ non-parasitic on host. AHC = Australian Helminth Collection, South Australian Museum; QM = Queensland Museum, Brisbane; SAM = South Australia Museum.

| Parasite | Authority | Host | Accession numbers |
|---|---|---|---|
| ACANTHOCEPHALA | | | |
| RHADINORHYNCHIDAE | | | |
| *Rhadinorhynchus pristis* * | Luhe, 1911 | Sa | QMG212206 |
| CESTODA | | | |
| BOTHRIOCEPHALIDAE | | | |
| *Bothriocephalus manubriformis* | Linton, 1889 | SaBk | |
| DASYRHYNCHIDAE | | | |
| *Callitetrarhynchus gracilis* * † # | Rudolphi, 1819 | SaBkBl | QMG212785, SAM17410, 17417, 18495, 18496 |
| *Floriceps minacanthus* * † | Campbell & Beveridge,1987 | SaBk | AHC17411, 17414 |
| OTOBOTHRIDAE | | | |
| *Otobothrium dipsacum* * † # | Linton, 1897 | SaBkBl | QMG212165, 212166, 212798, 212799, 212800 |
| *Otobothrium* sp. † | | Sa | |
| PTEROBOTHRIDAE | | | |
| *Pterobothrium heterocanthum* † | Diesing, 1850 | SaBk | QMG212801, 212802 |
| TENTACULARIIDAE | | | |
| *Nybelinia* sp. † | | Sa | |
| COPEPODA | | | |
| CALIGIDAE | | | |
| *Caligus* sp. * † | | SaBk | |
| EURYPHORIDAE | | | |
| *Gloiopotes huttoni* | (Thomson, 1889) | SaBkBlSt | |
| PENNELLIDAE | | | |
| *Pennella instructa* | Wilson, 1917 | SaBkSt | |
| PHILICHTHYIDAE | | | |
| *Philichthys xiphiae* † | Steenstrup, 1861 | Sa | |
| CRUSTACEA | | | |
| LEPADIDAE | | | |
| *Conchoderma virgatum* * ‡ | (Spengler, 1790) | SaBk | |
| DIGENEA | | | |
| ACANTHOCOLPIDAE | | | |
| *Stephanostomum* larva * † | Looss, 1899 | SaBk | |

TABLE 1 (*cont.*)

| | | | |
|---|---|---|---|
| DIDYMOZOIDAE | | | |
| *Angionematobothrium jugulare* * | Yamaguti, 1970 | SaBk | |
| *Glomeritrema subcuticola* * † | Yamaguti, 1941 | SaBk | QMG212173, 212789 |
| *Makairatrema musculicola* † # | Yamaguti, 1970 | SaBkBl | QMG212178, 212201, 212791, 212792 |
| *Metadidymozoon branchiale* | Yamaguti, 1970 | SaBk | QMG212202, 212793 |
| *Neodidymozooides microstoma* † | Yamaguti, 1970 | SaBl | QMG212168, 212169, 212796, 212797 |
| *Neodidymozoon macrostoma* * † | Yamaguti, 1970 | SaBkBl | QMG212174, 212175, 212203, 212204, 212795 |
| *Nematobothrium* sp. A * † | | SaBk | |
| *Nematobothrium* sp. B * † | | SaBk | QMG212794 |
| *Neotorticaecum* larva † | Kurochkin & Nikolaeva,1978 | Sa | |
| *Torticaecum* larva * † | Yamaguti, 1971 | SaBk | |
| HIRUDINELLIDAE | | | |
| *Hirudinella marina* * † | (Garcin, 1730) | SaBk | QMG212790 |
| SANGUINICOLIDAE | | | |
| *Cardicola grandis* † # | Lebedev & Mamaev, 1968 | SaBkBl | QMG212205, 212783, 212784 |
| *Cardicola* sp. * † # | | BkBl | QMG212786, 212787 |
| MONOGENEA | | | |
| CAPSALIDAE | | | |
| *Capsaloides cristatus* * | Yamaguti, 1968 | Bk | QMG212782 |
| *Capsaloides istiophori* * | Yamaguti, 1968 | SaBk | QMG212195 |
| *Capsaloides tetrapteri* * † # | Yamaguti, 1968 | SaBkBl | QMG212196, 212197, 212788 |
| *Tristomella pricei* | Price, 1960 | SaBkBlSt | QMG212198, 212199, 212200, 212803, 212804 |
| NEMATODA | | | |
| SPIRURIDAE | | | |
| *Camallanus* sp. * † | | SaBk | QMG212780, 212781 |
| ANISAKIDAE | | | |
| *Hysterothylacium pelagicum* | Deardorff & Overstreet,1982 | Bk | QMGL10113 |
| *Maricostula cenatica* | Bruce & Cannon, 1989 | St | QMGL10140 |
| *Maricostula histiophori* | (Yamaguti, 1935) | Sa | QMGL10114, 10115 |
| *Maricostula makairi* * | Bruce & Cannon, 1989 | Bk | QMGL10111, 10112 |
| *Maricostula tetrapteri* | Bruce & Cannon, 1989 | St | QMGL10143 |

ground (Table 1), indicates continuous exposure and accumulation with latitude (= time). That is, the distribution of *Neodidymozoon macrostoma* is consistent with southerly migration of juvenile black marlin between Cairns and Cape Moreton. Also, adult black marlin are not infected in the extra-reefal waters adjacent to Lizard I. but acquire their infections elsewhere, preceding arrival in these waters by a period exceeding that required for the parasite to mature.

The black marlin, with an unusually high infection of nematodes and its stomach unable to be everted, had been previously captured (59 days earlier) and discussions with the person who had first captured this fish indicated that the damage was inflicted by a tagging pole penetrating the body cavity. The infection may, therefore, have accumulated over this short period and the anatomy of these fishes suggests a mechanism, the ability to evert the stomach, for the removal of parasites (and perhaps fish bones, etc).

Sailfish and juvenile black marlin are seasonally abundant in areas where large mixed schools of baitfish occur in the shallow nearshore waters (Williams, 1990). These schools are dominated by pilchards, *Amblygaster sirm*, herrings, *Sardinella* spp., and yakkas, *Decapterus* sp. Black marlin were more likely to select pilchards from these schools whereas sailfish were far less likely to do so. In general, sailfish had a more diverse feeding strategy than black marlin which may account for their more diverse parasite fauna.

The parasites identified from striped and blue marlin, through less exhaustive dissections, demonstrate the likelihood of parasite faunas from these fish showing similarities to those of sailfish and black marlin.

## ACKNOWLEDGEMENTS

I am grateful to the many fishermen who provided the majority of fish for examination and Mike Cappo (Australian Institute of Marine Science) who assisted with many dissections. Several parasitologists assisted with parasite identifications and I thank Bob Lester (University of Queensland), Klaus Rhode (University of New England), Lester Cannon and Niel Bruce (Queensland Museum), Ian Beveridge (University of Melbourne) and David Blair (James Cook University of North Queensland) and the staff at

TABLE 2. The prevalence (P - %) and mean intensity (I), with associated standard deviation (SD) and range (RA), for each parasite infecting black marlin and sailfish from fishing grounds along the Queensland coast.

| Parasites of Black Marlin | Cape Bowling Green n = 33 | | | | Cape Moreton n = 11 | | | | Cairns n = 2 | | Dunk Island n = 4 | | | | Lizard Island n = 13 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | P | I | SD | RA | P | I | SD | RA | P | RA | P | I | SD | RA | P | I | SD | RA |
| *Bothriocephalus manubriformis* | 71.9 | 6.3 | 7.2 | 1-33 | 72.7 | 4.5 | 3.0 | 2-10 | 50 | 3 | 100 | 6.3 | 6.6 | 2-16 | 27.3 | 6.3 | 5.5 | 1-12 |
| *Callitetrarhynchus gracilis* | 6.1 | 5.5 | 3.5 | 3-8 | 9.1 | 1.0 | | | 0 | | 0 | | | | 7.7 | 1.0 | | |
| *Floriceps minacanthus* | 48.5 | 2.8 | 2.1 | 1-8 | 54.5 | 3.7 | 3.0 | 1-9 | 50 | 6 | 50.0 | 3.5 | 3.5 | 1-6 | 15.4 | 4.0 | 4.2 | 1-7 |
| *Otobothrium dipsacum* | 12.1 | 1.5 | 0.6 | 1-2 | 9.1 | 1.0 | | | 0 | | 0 | | | | 38.5 | 2.0 | 1.0 | 1-3 |
| *Pterobothrium heterocanthum* | 6.1 | 4.0 | 4.2 | 1-7 | 0 | | | | 0 | | 0 | | | | 0 | | | |
| *Caligus* sp. | 87.1 | 11.0 | 9.6 | 1-41 | 80.0 | 28.5 | 17.4 | 11-60 | 50 | 2 | 50.0 | 4.5 | 3.5 | 2-7 | 0 | | | |
| *Gloiopotes huttoni* | 93.9 | 93.2 | 132.0 | 3-736 | 100 | 117.5 | 81.9 | 6-329 | 50 | 24 | 100 | 57.5 | 56.0 | 7-107 | 76.9 | 67.9 | 46.5 | 2-141 |
| *Pennella instructa* | 21.2 | 16.4 | 24.1 | 1-66 | 36.4 | 6.3 | 4.3 | 2-12 | 0 | | 50.0 | 67.5 | 91.2 | 3-132 | 46.2 | 24.0 | 29.7 | 4-82 |
| *Conchoderma virgatum* | 3.0 | 26.0 | | | 9.1 | 21.0 | | | 0 | | 25.0 | 9.0 | | | 15.4 | 5.5 | 4.9 | 2-9 |
| *Angionemato-bothrium jugulare* | 3.0 | 1.0 | | | 9.1 | 3.0 | | | 0 | | 25.0 | 6.0 | | | 0 | | | |
| *Glomeritrema subcuticola* | 93.9 | 62.5 | 35.6 | 15-132 | 100 | 72.3 | 56.0 | 11-211 | 100 | 55-122 | 100 | 42.5 | 19.8 | 16-64 | 84.6 | 202.3 | 192.5 | 55-660 |
| *Makairatrema musculicola* | 9.1 | 3.0 | 3.5 | 1-7 | 0 | | | | 0 | | 0 | | | | 0 | | | |
| *Metadidymozoon branchiale* | 24.2 | 11.3 | 19.2 | 1-58 | 63.6 | 15.9 | 18.0 | 2-48 | 0 | | 25.0 | 1.0 | | | 0 | | | |
| *Neodidymozoon macrostoma* | 87.9 | 20.7 | 26.9 | 1-128 | 90.9 | 32.8 | 23.3 | 14-77 | 100 | 10-30 | 100 | 9.5 | 9.6 | 2-22 | 38.5 | 37.8 | 32.4 | 1-79 |
| *Nematobothrium* sp. A | 15.2 | 3.8 | 4.1 | 1-11 | 27.3 | 2.7 | 1.5 | 1-4 | 0 | | 75.0 | 3.3 | 2.5 | 1-6 | 0 | | | |
| *Nematobothrium* sp. B | 24.2 | 4.3 | 2.9 | 1-10 | 36.4 | 7.5 | 6.1 | 2-15 | 100 | 4-5 | 100 | 3.8 | 1.9 | 1-5 | 15.4 | 3.5 | 2.1 | 2-5 |
| *Torticaecum* larva | 3.0 | 1.0 | | | 0 | | | | 0 | | 0 | | | | 0 | | | |
| *Hirudinella marina* | 0 | | | | 0 | | | | 0 | | 0 | | | | 61.5 | 5.9 | 5.6 | 1-17 |
| *Cardicola* grandis | 45.5 | 2.1 | 2.1 | 1-8 | 45.5 | 2.0 | 2.2 | 1-6 | 0 | | 0 | | | | 7.7 | 5.0 | | |
| *Capsaloides cristatus* | 0 | | | | 9.1 | 7.0 | | | 0 | | 0 | | | | 0 | | | |
| *Capsaloides istiophori* | 12.1 | 2.5 | 2.4 | 1-6 | 40.0 | 63.0 | 85.0 | 11-190 | 0 | | 0 | | | | 0 | | | |
| *Capsaloides tetrapteri* | 3.0 | 24.0 | | | 10.0 | 1.0 | | | 0 | | 0 | | | | 0 | | | |
| *Tristomella pricei* | 93.9 | 17.1 | 22.2 | 1-89 | 100 | 86.8 | 72.5 | 10-245 | 100 | 21-32 | 100 | 75.3 | 89.6 | 22-209 | 84.6 | 77.7 | 65.7 | 14-253 |
| *Camallanus* sp. | 33.3 | 3.0 | 2.1 | 1-8 | 0 | | | | 100 | 1 | 50.0 | 3.5 | 0.7 | 3-4 | 15.4 | 1.0 | 0.0 | |
| Adult nematodes | 63.6 | 88.7 | 221.1 | 1-854 | 81.8 | 14.0 | 12.4 | 1-43 | 50 | 16 | 100 | 2.8 | 2.2 | 1-6 | 30.8 | 19.0 | 10.9 | 9-33 |

| Parasites of Sailfish | Cape Bowling Green n = 24 | | | | Cape Moreton n = 19 | | | | Dunk Island n = 3 | | Whitsundays n = 6 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | P | I | SD | RA | P | I | SD | RA | P | RA | P | I | SD | RA |
| *Rhadinorhynchus pristis* | 4.2 | 1.0 | | | 0 | | | | 0 | | 0 | | | |
| *Bothriocephalus manubriformis* | 83.3 | 8.7 | 12.5 | 1-55 | 100 | 66.0 | 107.3 | 3-471 | 100 | 4-74 | 100 | 19.2 | 20.6 | 2-58 |
| *Callitetrarhynchus gracilis* | 8.3 | 4.5 | 2.1 | 3-6 | 11.1 | 1.5 | 0.7 | 1-2 | 33.3 | 24 | 16.7 | 9.0 | | |
| *Floriceps minacanthus* | 50.0 | 14.9 | 11.7 | 2-34 | 16.7 | 9.0 | 13.9 | 1-25 | 66.7 | 8-19 | 100 | 13.7 | 10.9 | 2-32 |
| *Otobothrium dipsacum* | 29.2 | 9.7 | 15.5 | 1-44 | 5.3 | 1.0 | | | 33.3 | 3 | 66.7 | 7.3 | 10.0 | 1-22 |
| *Obothrium* sp. | 0 | | | | 0 | | | | 0 | | 83.3 | 150.0 | 130.9 | 7-267 |
| *Pterobothrium heterocanthum* | 4.2 | 1.0 | | | 0 | | | | 0 | | 16.7 | 1.0 | | |

TABLE 2. (*cont.*)

| | Cape Bowling Green n = 24 | | | | Cape Moreton n = 19 | | | | Dunk Island n = 3 | | Whitsundays n = 6 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Parasites of Sailfish | P | I | SD | RA | P | I | SD | RA | P | RA | P | I | SD | RA |
| *Nybelinia* sp. | 12.5 | 3.3 | 3.2 | 1-7 | 5.3 | 19.0 | | | 0 | | 50.0 | 29.3 | 6.7 | 25-37 |
| *Caligus* sp. | 82.6 | 39.3 | 31.1 | 2-97 | 100 | 138.8 | 142.6 | 6-443 | 100 | 3-6 | 83.3 | 80.0 | 75.2 | 4-193 |
| *Gloiopotes huttoni* | 90.5 | 16.8 | 12.6 | 2-48 | 92.9 | 17.0 | 13.7 | 2-49 | 100 | 6-10 | 100 | 57.0 | 63.8 | 8-153 |
| *Pennella instructa* | 33.3 | 3.5 | 3.5 | 1-10 | 84.2 | 8.4 | 7.3 | 2-26 | 33.3 | 4 | 66.7 | 5.3 | 7.2 | 1-16 |
| *Conchoderma virgatum* | 4.2 | 1.0 | | | 21.1 | 3.3 | 1.0 | 2-4 | 0 | | 0 | | | |
| *Stephanostomum* larva | 0 | | | | 0 | | | | 0 | | 50.0 | 9.3 | 6.1 | 4-16 |
| *Angionemato-bothrium jugulare* | 8.3 | 2.5 | 2.1 | 1-4 | 21.1 | 2.0 | 2.0 | 1-5 | 33.3 | 4 | 0 | | | |
| *Glomeritrem a subcuticola* | 4.2 | 1.0 | | | 0 | | | | 0 | | 0 | | | |
| *Makairatrem a musculicola* | 20.8 | 12.6 | 24.3 | 1-56 | 26.3 | 21.6 | 26.5 | 2-67 | 0 | | 0 | | | |
| *Metadidymozoon branchiale* | 72.7 | 48.9 | 98.6 | 1-369 | 63.2 | 226.3 | 407.7 | 1-1226 | 0 | | 60.0 | 24.3 | 13.7 | 15-40 |
| *Neodidymozoon macrostoma* | 75.0 | 7.3 | 9.7 | 1-42 | 89.5 | 10.2 | 12.5 | 2-47 | 66.7 | 1-3 | 50.0 | 2.7 | 2.1 | 1-5 |
| *Nematobothriu* sp. A | 47.4 | 5.4 | 5.0 | 1-15 | 61.1 | 4.3 | 3.3 | 1-13 | 66.7 | 2-3 | 33.3 | 3.5 | 0.7 | 3-4 |
| *Nematobothriu* sp. B | 8.3 | 2.5 | 2.1 | 1-4 | 36.8 | 2.0 | 1.0 | 1-4 | 33.3 | 1 | 16.7 | 2.0 | | |
| *Neotorticaecum* larva | 0 | | | | 0 | | | | 0 | | 16.7 | 6.0 | | |
| *Torticaecum* larva | 16.7 | 5.8 | 4.0 | 1-10 | 0 | | | | 33.3 | 2 | 50.0 | 6.3 | 3.2 | 4-10 |
| *Hirudinella marina* | 4.2 | 1.0 | | | 0 | | | | 0 | | 0 | | | |
| *Cardicola grandis* | 82.6 | 19.3 | 14.0 | 1-51 | 35.3 | 14.8 | 14.8 | 1-38 | 100 | 4-9 | 66.7 | 7.3 | 10.5 | 2-23 |
| *Capsaloides istiophori* | 42.9 | 7.3 | 7.0 | 1-23 | 78.9 | 51.0 | 64.9 | 2-194 | 0 | | 40.0 | 29.5 | 20.5 | 15-44 |
| *Capsaloides tetrapteri* | 23.8 | 2.8 | 1.9 | 1-6 | 57.9 | 26.1 | 46.7 | 1-156 | 0 | | 40.0 | 7.5 | 2.1 | 6-9 |
| *Tristomella pricei* | 55.0 | 9.9 | 8.5 | 1-24 | 86.7 | 13.9 | 15.5 | 1-47 | 33.3 | 1 | 60.0 | 1.3 | 0.6 | 1-2 |
| *Camallanus* sp. | 58.3 | 4.0 | 2.2 | 1-8 | 5.3 | 2.0 | | | 66.7 | 2-4 | 16.7 | 10.0 | | |
| Adult nematodes | 66.7 | 28.9 | 93.9 | 2-381 | 73.7 | 3.0 | 2.6 | 1-11 | 100 | 1-5 | 66.7 | 43.3 | 29.6 | 2-70 |

TABLE 3. Stomach contents of sailfish and black marlin from Queensland coastal waters. Count is the number of food items of each category and (in brackets) the percentage contribution of that food item to the diet of all fish examined. Prevalence is the percentage of fish with that food item. * - includes bills and mandibles from LI fish with values based on LI fish only.

| Sailfish (n=34) | Count (%) | Prevalence | Black marlin (n=41) | Count (%) | Prevalence |
|---|---|---|---|---|---|
| *Amblygaster sirm* | 23 (3) | 30 | *Amblygaster sirm* | 132 (78) | 66 |
| *Tylosurus* sp. | 18 (2) | 27 | *Sardinella gibbosa* | 25 (15) | 19 |
| *Balistoides* sp. | 425 (49) | 15 | *Decapterus* sp. | 4 (2) | 7 |
| *Sardinella* spp. | 7 (1) | 12 | *Sarda* sp. | 3 (2) | 5 |
| *Decapterus* sp. | 5 (1) | 9 | *Carangoides* sp. | 1 (1) | 2 |
| Tetraodontidae | 373 (43) | 6 | *Chirocentrus dorab* | 1 (1) | 2 |
| *Loligo* sp. | 2 (1) | 6 | *Sphyraena* sp. | 1 (1) | 2 |
| *Scomberoides* sp. | 2 (1) | 3 | empty | - - | 15 |
| *Hyperlophus* sp. | 3 (1) | 3 | billfish remains * | 4 - | 31 |
| *Paramonacanthus* sp. | 1 (1) | 3 | | | |
| *Lactoria* sp. | 1 (1) | 3 | | | |
| empty | - - | 6 | | | |

the US Helminthological Museum, Beltsville, Maryland. Billfish remains in the stomachs of black marlin were identified by Harry Fierstein (Biological Sciences Department, California Polytechnic State University, San Luis Obispo).

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# VERTEBRATE FAUNA OF CANNABULLEN PLATEAU: A MID-ALTITUDE RAINFOREST IN THE AUSTRALIAN WET TROPICS

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Williams, S.E., Vernes, K. & Coughlin, J. 1999 06 30: Vertebrate fauna of Cannabullen Plateau: a mid-altitude rainforest in the Australian wet tropics. *Memoirs of the Queensland Museum* **43**(2): 849-858. Brisbane. ISSN 0079-8835.

This paper reports on a vertebrate fauna survey undertaken at the Cannabullen Section of Tully Gorge National Park in the north Queensland Wet Tropics. A team of 6 biologists surveyed the plateau and adjacent Cochable Creek over 20 days in November 1993 using a combination of standardised methods including mammal trapping, active reptile searches, spotlighting and bird censuses. Additional miscellaneous observations were also included. Ninety-six species of vertebrate were detected (12 mammals, 52 birds, 22 reptiles and 10 amphibians) of which 29 were endemic to the Wet Tropics Region. Thirty-nine species were considered to be significant with respect to the conservation of the World Heritage values of the region, with 8 of these recognised as being rare or endangered in Queensland. The survey extended the known altitudinal range of 6 species endemic to the Wet Tropics to well below their previously recognised limits. ❐ *Vertebrate fauna, Cannabullen Plateau, rainforest, survey, Queensland, Australia.*

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Although reasonable information now exists regarding the regional distributions of most Wet Tropics vertebrates, there is a paucity of detailed local-scale surveys reported in the literature. Only a handful of field studies have published detailed descriptions of the vertebrate assemblages occurring in a specific area within the Wet Tropics (Gill, 1970; Winter et al., 1992; Kutt et al., 1995a,b; Williams et al., 1993; Williams & Marsh, 1998). Instead, most published work has been based on a synthesis of existing information, mainly unpublished, gathered by many researchers over many years (e.g. Kikkawa, 1982; Winter et al., 1984; Winter, 1988; papers in Nix & Switzer, 1991; McDonald, 1992; Covacevich & McDonald, 1993; Werren, 1993; Williams et al., 1996; Williams, 1997; Winter, 1997). Such examinations provide valuable insights, however, most of the primary survey work on which these broad-scale studies are based have concentrated on either the upland rainforests (above 600m) or the lowland coastal rainforest (below 100m). Few studies have been undertaken in the mid-elevation rainforest (200-600m), largely as a consequence of the relative inaccessibility of the forests and the steep terrain in much of this zone (McDonald, 1992; Williams et al., 1996).

In a review on vertebrate distributions and biodiversity in the Wet Tropics, Williams et al. (1996) concluded that one of the most important environmental gradients in the region was altitude, and identified mid-altitudes as being the poorest surveyed areas. The lower altitudinal tolerances of many Wet Tropics species are uncertain due to the lack of distributional data at mid-elevations. Fauna surveys within this altitudinal range are important, since they illuminate the changes occurring across the altitudinal gradient. Many of the regionally-endemic species are upland species and accurate information about their altitudinal limits is crucial when interpreting patterns of biogeography. Furthermore, the altitudinal gradient islinked tightly to the understanding of patterns of biodiversity in the region, especially the influences of historical rainforest contractions during the Pleistocene (Williams, 1997; Williams & Pearson, 1997; Winter, 1997; Williams & Hero, 1998).

More than 70% of rainforest in the Wet Tropics has been altered by logging, with the relatively flat, or gently sloping ground being most affected (Winter et al., 1987). Consequently, most of the regional data on vertebrate distributions originates from forests which have been subjected to selective logging. Selective logging

changes the physical structure of the forest (Winter et al., 1987) which in turn influences the composition of the vertebrate community (Pahl et al., 1988; Laurance & Laurance, 1996; Williams & Marsh, 1998; Williams et al., 1996). As most of the undisturbed rainforest remaining in the region lies on the rugged escarpments within the mid-altitudinal range, surveys of these areas will provide important information on both undisturbed and mid-altitudinal faunal assemblages.

This paper reports on a fauna survey conducted at the Cannabullen Section of Tully Gorge National Park on the southern slopes of the Atherton Tableland in N Queensland. The section of the national park is comprised largely of Cannabullen Plateau, a mid-elevation (420-480m ASL) unlogged rainforest. The plateau has escaped logging and the associated fragmentation by roads and snig-tracks because deep gorges and rugged terrain surround it. Few fauna surveys have been undertaken in the national parks of the Wet Tropics and none in the vicinity of Cannabullen. As such, this study represents an important addition to the knowledge of vertebrate fauna within the national parks estate. Additionally, the study adds to our knowledge of the vertebrate fauna in mid-elevation unlogged rainforest in the Australian Wet Tropics.

## METHODS

Cannabullen Plateau is situated on the southern escarpment of the Atherton Tableland, approximately 15km SE of Ravenshoe (17°42'S 145°37'E). The plateau is relatively flat and consists of approximately 12,500ha of rainforest (mesophyll vine forest) on basaltic soils.

A team of 6 biologists surveyed the vertebrate fauna of the plateau and adjacent Cochable Ck over 20 days in November 1993. Sampling was conducted at 3 primary sites on the plateau: Site P1 near the southern end, Site P2 in the centre and Site P3 on the northern end of the plateau. Two secondary sites were surveyed on Cochable Ck which defines the western and southern edge of the plateau. Site C1 (third order stream) was situated below the camp at the southern end of the plateau while Site C2 (second order stream) was in the headwaters of Cochable Creek at the northern end of the plateau. Table 1 summarises the exact site localities, altitudes and habitat descriptions for each site. Cannabullen Creek in the gorge on the east of the plateau was only visited once due to the relative inaccessibility of that gorge.

Each plateau sites was sampled using a standardised combination of methods, including mammal trapping, active searches, spotlighting and bird transects. Sampling at the two creek sites consisted of bat mist-netting and frog transects. In addition to the standardised sampling all miscellaneous records were recorded and miscellaneous searches were conducted in any areas or microhabitats not represented in the primary sites, including several nights of bat mist-netting (two nets) at each of the creek sites. Voucher specimens were taken for species where there was any doubt about identification and lodged with the Queensland Museum (specimen numbers QMJ59879-QMJ59901).

Five trapping grids were established at each site (P1, P2 & P3) with at least 200m between adjacent grids. Each grid consisted of 20 small mammal traps (Elliott type A) and 2 wire cage traps (Mascot Wire, 30×30×60cm, folding, treadle type). The traps were set in two parallel lines 10m apart with 10 Elliot traps (5m apart) along each line. The two cage traps were placed between the lines at the second trap in from each end. Traps were baited with a mixture of rolled oats and vanilla essence, and checked and re-baited each morning for four nights at each site. Therefore, a total of 440 trap-nights were conducted at each of the three sites on the plateau. All animals caught were identified, tagged with individually numbered monel metal ears tags, sexed, weighed and released at the trap site.

Standardised spotlighting transects were conducted to sample all nocturnal vertebrate fauna. A single spotlighting transect approximately 1km long was established at each site. Each transect was sampled on three nights. Spotlighting was standardised to reduce biases in a technique which has intrinsic high variability (using methods described in Williams, 1995). Spotlighting was conducted between 1900h and 2400h. We used two 30W hand-held spotlights and binoculars to identify animals on all transects. For each observation of an animal the time, species, position along the transect, estimated distance from the transect, estimated height and the method of detection (call, sight, heard movement) were recorded.

Bird surveys utilising both sightings and calls were conducted over the same transects as the spotlighting transect. Each transect was surveyed three times by the same two people. Each census took between 90 and 120min and was undertaken

TABLE 1. Site localities and habitat descriptions. Vegetation types follow Tracey & Webb (1975).

| Site | AMG | Altitude | Habitat |
|---|---|---|---|
| C1 | 352400 / 8042200 | 340 | Third order stream; wide canopy break (30m), large boulders, some bedrock, riffles, waterfalls and large pools |
| C2 | 351900 / 8043600 | 410 | Second order stream, narrow canopy break (5m), small pools, riffles, small boulders, number of small first order gullies |
| P1 | 352600 / 8042300 | 420 | Mixed mesophyll vine forest (type 1a/2a) – heavily cyclone disturbed; dense understorey |
| P2 | 352600 / 8042900 | 460 | Mixed mesophyll vine forest (type 1a/2a) – less cyclone damage; patchy dense understorey |
| P3 | 352300 / 8043500 | 490 | Mixed mesophyll vine forest (type 1a/2a) – little cyclone damage; open understorey |

in the 2h following dawn. Numbers of individual birds were not recorded.

Surveys for stream-dwelling frogs were carried out along the creek at Sites C1 and C2. Each transect consisted of a 200m length of creek and was surveyed three times by two people using spotlights and head torches between 1700h and 2400h. The numbers of individuals were recorded on each survey, except when a large breeding chorus was encountered and abundances were estimated.

Active searches for herpetofauna consisted of two people walking along the standard transects (approximately 10m wide) at each site and recording all individuals that were visible and also by searching actively under logs, bark, leaf litter etc. The 1km transect at each site was surveyed three times, on different days. Searches were not carried out in rain or during times of heavy cloud cover.

## RESULTS

A total of 96 species of vertebrates were recorded during the survey comprising 12 mammals, 52 birds, 22 reptiles and 10 frogs (Table 2; see Appendix for relative abundances at each site and current conservation status of each species). Species richness was relatively uniform over the plateau with only minor differences in assemblage structure between the three primary plateau sites (Table 2). The cumulative species curve suggests that the total number of species was plateauing after surveying the 5 sites (Fig. 1). Bootstrap estimates of total species richness suggests that the study area contains approximately 109 species (Fig. 1). Therefore, we estimate that the survey recorded 88% of the total species richness.

Twenty-nine of the observed species or 30% of the total are endemic to the Wet Tropics region. Nearly 41% of these species (39 species) are considered to be very important species (VIS) with respect to the conservation of the world heritage values of the region (Williams et al., 1996; see Table 4 for VIS definition). Eight of these species are currently recognised as being rare, vulnerable or endangered under the Queensland Nature (Wildlife) Regulation (1994) (Table 2).

Five species of birds (Tooth-billed Bowerbird; Bowers Shrike-thrush; Australian Fernwren; Bridled Honeyeater; Atherton Scrubwren) and one gecko (*Carphodactylus laevis*) were observed well below the altitudinal limits given in Nix & Switzer (1991). All of these 6 species were thought to be restricted to above 600m ASL using recorded point locality data (Crome & Nix, 1991; Covacevich & McDonald, 1991). However, broad distributional data suggest that four of the bird species are known to occur down to 450m (Gill, 1970) and *C. laevis* is known to occur down to 300m (Covacevich & McDonald, 1993). Unfortunately, neither of these papers report point localities. Other noteworthy records on Cannabullen Plateau were the relatively high numbers of Musky Rat-kangaroos, Cassowaries and rare and/or endangered frogs. Two species of declining frogs (Richards et al., 1993) (*Litoria nannotis, L. rheocola*) were observed in reasonable numbers (Appendix), as were two rare microhylid frogs (*Cophixalus infacetus, Sphenophryne robusta*).

Although the vertebrate assemblages were relatively uniform throughout the plateau there were some differences between sites that are of ecological interest. Two species of mammals (*Melomys cervinipes, Uromys caudimaculatus*) and one reptile (*Saproscincus basilisicus*) were more abundant in the southern parts of the plateau, while 3 species of skinks were more abundant in the northern sites (*Carlia rubrigularis, Lampropholis coggeri, Gnypetoscincus queenslandiae*). The frog assemblages at the two

creek sites (Cochable Ck) were very different, reflecting differences in the microhabitats at each site. Site C1 was characterised by large pools with high flow and rocky substratum, and supported high numbers of stream dwelling hylid frogs (*Litoria genimaculata*, *L. lesueuri*, *L. rheocola*, *L. nannotis*) (Appendix). Site C2 was a smaller creek with small pools, fewer boulders and a more closed canopy. There were only a few individuals of each species of stream-dwelling hylid present at Site C2, however, there was a more diverse complement of microhylid frogs (*Cophixalus infacetus*, *Sphenophryne robusta*) than at C1. Water dragons (*Physignathous lesueuri*) were also much more common in the southern, larger section of the creek (Site C1). It was of interest that all sites on the plateau had sympatric populations of both Lewin's Honeyeaters and Yellow-spotted Honeyeaters, two species that are usually thought to be altitudinally allopatric (Longmore, 1991).

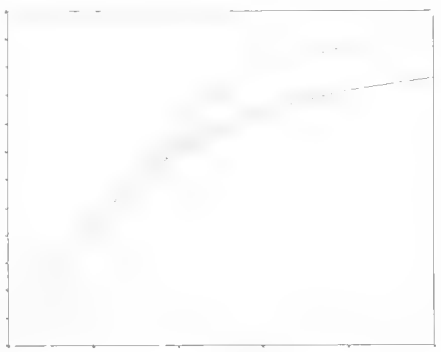


FIG. 1. Mean cumulative species curve for survey sites based on Monte-Carlo simulations of cumulative species counts over the five sites (solid line) and bootstrap estimate of species richness (dashed line). Both estimates are constructed using the mean of 1000 randomised runs using the program 'Species Diversity & Richness' (Henderson & Seaby 1997).

## DISCUSSION

The species richness of terrestrial vertebrates observed on Cannabullen Plateau may seem low considering that it lies within a region containing approximately 700 species (Williams et al., 1996). However, the plateau is very flat and the vegetation is relatively uniform. A diversity of almost 100 species of vertebrates is high given the lack of coarse habitat heterogeneity. For example, there are no large waterbodies, swamps, rocky outcrops or patches of non-rainforest vegetation which often increase dramatically the number of species in a given area (Williams et al., 1996).

Since Cannabullen Plateau is entirely rainforest and sufficiently distant from other vegetation types so as not to be influenced by non-rainforest species assemblages, this survey provides an estimate of true local-scale species richness within the rainforest. The cumulative species curve and bootstrap estimate of total species richness both suggest that the survey did record a large portion of the species present. Local-scale species richness is affected by a number of processes including regional species richness, habitat heterogeneity and the movements of individuals from adjoining habitats (mass-effect) (Shmida & Wilson, 1985; Ricklefs & Schluter, 1993). Due to the highly fragmented and often narrow shape of rainforests within the region (Williams & Pearson, 1997), it is difficult to obtain estimates of rainforest species richness which are not influenced by adjoining habitats or the strong effects of coarse scale habitat heterogeneity (Williams et al., 1996; Williams & Marsh, 1998). This study provides baseline reliable estimates (Fig. 1) of both local and habitat species richness of mid-altitude rainforest without the confounding effects due to coarse habitat heterogeneity and mass-effects from adjoining habitats.

Although local species richness does not vary greatly between the three primary sites on the plateau, there are some subtle, but ecologically significant, differences in the relative abundances of several species (see Appendix). These differences are probably the result of changes in the vegetation structure between the southern and northern ends of the plateau. It is well known that vegetation structure influences the assemblage structure of vertebrates (Southwood, 1996). The southern end of the plateau has been disturbed heavily by cyclones, whereas the northern end is much more protected and has suffered considerably less damage. This has resulted in a gradient in vegetation structure from the southern end which has a more open canopy, very dense middle layer and a dense lower shrub layer to a more closed canopy and much more open shrub and ground layers in the northern end of the plateau. Although these changes are patchy and subtle compared to the overall vegetation structure, they are seemingly significant enough to have influenced the abundances of several

TABLE 2. Summary of species richness at each site for each taxonomic class including: total number of species, number of regionally-endemic species, number of rare, vulnerable and endangered species listed under the Nature Conservation (Wildlife) Regulation (1994) and the number of species of conservation significance to the region (Very Important Species (VIS) are either listed rare, vulnerable or endangered and/or are regionally-endemic species or subspecies — after Williams et al., 1996). n/a = not applicable (no standardised bird surveys at these sites).

| | Sites | | | | | Total |
|---|---|---|---|---|---|---|
| | C1 | C2 | P1 | P2 | P3 | |
| **Mammals** | | | | | | |
| Total | 4 | 3 | 10 | 10 | 7 | 12 |
| Rare, vulnerable & endangered | - | - | 1 | - | - | 1 |
| Regional endemics | 1 | - | 2 | 1 | 1 | 2 |
| VIS | 1 | 2 | 3 | 2 | 1 | 3 |
| **Birds** | | | | | | |
| Total | n/a | n/a | 38 | 41 | 42 | 52 |
| Rare, vulnerable & endangered | n/a | n a | 1 | - | 1 | 1 |
| Regional endemics | n/a | n/a | 8 | 9 | 8 | 11 |
| VIS | n/a | n/a | 15 | 16 | 16 | 19 |
| **Reptiles** | | | | | | |
| Total | 11 | 9 | 14 | 7 | 11 | 22 |
| Rare, vulnerable & endangered | - | - | 1 | - | 1 | 1 |
| Regional endemics | 5 | 4 | 8 | 6 | 8 | 9 |
| VIS | 5 | 4 | 8 | 6 | 8 | 9 |
| **Amphibians** | | | | | | |
| Total | 4 | 9 | 5 | 2 | - | 10 |
| Rare, vulnerable & endangered | 3 | 5 | 2 | 1 | - | 5 |
| Regional endemics | 2 | 7 | 4 | 1 | - | 7 |
| VIS | 3 | 8 | 4 | 1 | - | 8 |
| Total number of species | 20 | 21 | 67 | 60 | 60 | 96 |

species including some of the small mammals (*Melomys cervinipes, Uromys caudimaculatus*) and skinks (*Carlia rubrigularis, Lampropholis coggeri, Saproscincus basilisicus, Gnypetoscincus queenslandiae*) (Table 2, Appendix). Similarly, there are large differences in the vertebrate assemblages between Sites C1 and C2 due to the large differences in the habitat structure of the creek. The stream-dwelling hylid frogs, water dragons (*Physignathus lesueurii*) and water skinks (*Eulamprus quoyii*) are much more common in the rocky, higher flow habitat at C1 while microhylids are both more diverse and more abundant in the smaller headwaters at site C2 and at site P1. The known microhabitat preferences (Cogger, 1996) of these fauna reflect the pattern of distribution observed in this survey. For example, amongst the frogs detected, stream- dwelling hylids typically prefer swift-flowing rocky streams, while the microhylid species are usually associated with leaves and other debris on the rainforest floor, especially in moist areas (McDonald, 1992). Estimates of local abundances of birds were not accounted for in this study and, therefore, comparisons of the relative abundances of birds at each site could not be made.

The records of regionally endemic species at considerably lower altitudes than previously recognised are important for interpreting biogeographic patterns across the region. Analyses utilising climatic models (e.g. Nix & Switzer, 1991) are reliant on a relatively small number of records often biased towards areas of easy access. Eight regionally endemic bird species were previously recognised as being restricted to above 600m (Crome & Nix, 1991), yet this survey recorded five of these eight species at just over 400m. Our data agree with the general statements on bird distributions by Gill (1970) that many of the upland endemics are found at altitudes as low as 340m. The incorporation of these data would influence predicted climatic profiles and distributions for several species and may change the interpretation of the effects that historical climate fluctuations have had on these species. The lack of comprehensive, region-wide point data remains one of the most significant problems in analyses of vertebrate distributions in the region, especially in areas of difficult access.

Cannabullen Plateau contains many vertebrate species of conservation significance, with 41% of species having a Very-Important-Species (VIS) rating (Williams et al., 1996) and 30% of species being restricted to the Wet Tropics region (Table 2). In particular, there were good populations of two species of declining frogs (*Litoria nannotis, L. rheocola*). Upland areas above 600m ASL have always been considered to be the most

significant areas for regionally-endemic vertebrates in the Wet Tropics (Nix & Switzer, 1991). The results of this survey suggest that this significant zone should extend down to at least 400m ASL, similar to the scheme used in Winter et al. (1984). However, the plateau is unusual in that there is a considerable flat area of rainforest on highly fertile basalt at mid-altitudes. There is evidence that foliar nutrients are higher on the more fertile basaltic soils and that this produces differences in the structure of the faunal assemblages between basaltic and granitic soils (J. Kanowski, unpubl. data). Other surveys at mid-altitudes are needed to confirm the generality of these findings. The generality of these results are further limited by being based on a single, albeit comprehensive, survey. Since this national park contains such a large proportion of species of significant conservation value within the Wet Tropics, it represents a significant resource in the management and protection of the biodiversity and wilderness values of the region. The Cannabullen Plateau Section of Tully Gorge National Park, and the adjacent Elizabeth Grant Falls Section are relatively inaccessible at present because of the natural protection afforded by the surrounding topography and perhaps it would be best if this isolation were to be actively maintained.

## ACKNOWLEDGEMENTS

We thank Steve Comport, Jeff Middleton and Stephanie White for their endurance and hard work during the many trials involved in this expedition. We are indebted to the Wet Tropics Management Authority, Australian Geographic, and the Department of Tropical Environmental Studies and Geography (James Cook University) for their generous funding. Thanks are extended to the Queensland Departments of Environment and Natural Resources for permission to undertake the survey. Many thanks to John Winter and Alex Kutt for their suggestions and comments on the manuscript.

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## APPENDIX

List of species recorded during survey; conservation status defined by Nature Conservation (Wildlife) Regulation (1994) (NCR), regional endemics (END) and very important species (VIS) as defined by Williams et al. (1996) as being of significant conservation importance are indicated; overall relative abundance index at Cannabullen Plateau and abundances at each of the sites. Abundances are the total number of individuals observed at each site except for birds where the number represents the number of transects at each site that each species was recorded (max. 3). Abundance index is an estimate of relative abundance for each species on Cannabullen Plateau based on the combination of all methods and sites (Abund. Index): 1 = rare, only observed once or twice during entire survey; 2 = uncommon, observed several times, usually on several transects and sometimes at more than one site; 3 = common, observed on most transects at multiple sites; 4 = abundant, observed on most transects at most sites and usually with multiple numbers of individuals.

| Family | Species | Common | NCR | END | VIS | Abund. Index | Sites | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | C1 | C2 | P1 | P2 | P3 |
| Dasyuridae | *Antechinus flavipes* | Yellow-footed Antechinus | | | * | 2 | | 1 | 1 | 1 | |
| Peramelidae | *Perameles nasuta* | Long-nosed Bandicoot | | | | 3 | | | 5 | 9 | 5 |
| Petauridae | *Dactylopsila trivirgata* | Striped Possum | | | | 1 | | | 1 | | |
| Pseudocheiridae | *Pseudocheirops archeri* | Green Ringtail Possum | R | * | * | 1 | | | 1 | | |
| Potoroidae | *Hypsiprymnodon moschatus* | Musky Rat-kangaroo | | * | * | 4 | 1 | | 12 | 6 | 11 |
| Macropodidae | *Thylogale stigmatica* | Red-legged Pademelon | | | | 3 | | | 2 | 5 | 7 |
| Pteropodidae | *Nyctimene robinsoni* | Queensland Tube-nosed Bat | | | | 3 | 1 | | 3 | 3 | 3 |

| Family | Species | Common | NCR | END | VIS | Abund. Index | Sites | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | C1 | C2 | P1 | P2 | P3 |
| Muridae | *Hydromys chrysogaster* | Water Rat | | | | 1 | 1 | 1 | | | |
| Muridae | *Melomys cervinipes* | Fawn-footed Melomys | | | | 2 | | | 7 | 2 | |
| Muridae | *Rattus fuscipes* | Bush Rat | | | | 4 | | | 19 | 13 | 21 |
| Muridae | *Uromys caudimaculatus* | Giant White-tailed Rat | | | | 3 | | 1 | 4 | 2 | 2 |
| Suidae | *Sus scrofa* | Feral Pig | | | | 2 | 1 | | | 2 | 2 |
| Casuariidae | *Casuaris casuaris* | Southern Cassowary | E | | * | 2 | | | 1 | | 1 |
| Megapodiidae | *Alecturi lathami* | Australian Brush Turkey | | | | 2 | | | | 2 | 2 |
| Megapodiidae | *Megapodius reinwardt* | Orange-footed Scrubfowl | | | | 3 | | | 3 | 3 | 3 |
| Rallidae | *Rallina tricolor* | Red-necked Crake | | | | 1 | | | | 1 | |
| Columbidae | *Chalcophaps indica* | Emerald Dove | | | | 1 | | | | 1 | |
| Columbidae | *Lopholaimus antarcticus* | Topknot Pigeon | | | | 2 | 3 | | 1 | | |
| Columbidae | *Macropygia amboinensis* | Brown Cuckoo-Dove | | | | 3 | | | 3 | 3 | 3 |
| Columbidae | *Ptilinopus magnificus* | Wompoo Fruit-Dove | | | | 3 | | | 3 | 3 | 3 |
| Columbidae | *Ptilinopus regina* | Rose-crowned Fruit-Dove | | | | 2 | | | 1 | 1 | 1 |
| Columbidae | *Ptilinopus superbus* | Superb Fruit-Dove | | | | 3 | | | 3 | 3 | 3 |
| Cacatuidae | *Cacatua galerita* | Sulphur-crested Cockatoo | | | | 3 | | | 3 | 2 | 3 |
| Psittacidae | *Alisteris scapularis* | Australian King Parrot | | | * | 3 | | | 2 | 1 | 2 |
| Psittacidae | *Trichoglossus chlorolepidotus* | Scaly-breasted Lorikeet | | | | 3 | | | 2 | 3 | 2 |
| Psittacidae | *Trichoglossus haematodus* | Rainbow Lorikeet | | | | 3 | | | 3 | 2 | 3 |
| Cuculidae | *Cacomantis flabelliformis* | Fan-tailed Cuckoo | | | | 1 | | | | | 1 |
| Cuculidae | *Eudynamys scolopacea* | Common Koel | | | | 2 | | | 1 | | |
| Tytonidae | *Tyto multipunctata* | Lesser Sooty Owl | | * | * | 1 | | | 1 | | |
| Strigidae | *Ninox novaseelandiae* | Southern Boobook | | | * | 2 | | | 2 | 1 | 1 |
| Alcedinidae | Alcedo pusilla | Little Kingfisher | | | | 1 | | | | | 1 |
| Halcyonidae | *Dacelo novaeguineae* | Laughing Kookaburra | | | | 2 | | | 3 | 1 | 1 |
| Pittidae | *Pitta versicolor* | Noisy Pitta | | | | 2 | | | 1 | 1 | 1 |
| Campephagidae | *Coracina lineata* | Barred Cuckoo-Shrike | | | | 2 | | | | | 3 |
| Campephagidae | *Lalage leucomela* | Varied Triller | | | | 3 | | | 2 | 3 | 3 |
| Orthonychidae | *Orthonyx spaldingii* | Chowchilla | | * | * | 3 | | | 2 | 2 | 3 |
| Cinclosomatidae | *Psophodes olivaceus* | Eastern Whipbird | | | * | 3 | | | 3 | 2 | 3 |
| Pardalotidae | *Gerygone mouki* | Brown Gerygone | | | * | 4 | | | 3 | 3 | 2 |
| Pardalotidae | *Oreoscopus gutteralis* | Fernwren | | * | * | 1 | | | | 1 | |
| Pardalotidae | *Sericornis keri* | Atherton Scrubwren | | * | * | 1 | | | | 1 | 1 |
| Pardalotidae | *Sericornis magnirostris* | Large-billed Scrubwren | | | | 2 | | | 1 | 2 | 3 |
| Dicruridae | *Arses kaupi* | Pied Monarch | | * | * | 1 | | | 1 | | |
| Dicruridae | *Machaerirhynchus flaviventer* | Yellow-breasted Boatbill | | | * | 1 | | | | 1 | 1 |
| Dicruridae | *Monarcha melanopsis* | Black-faced Monarch | | | | 2 | | | 1 | | 2 |
| Dicruridae | *Monarcha trivirgatus* | Spectacled Monarch | | | | 3 | | | 2 | 2 | 2 |
| Petroicidae | *Heteromyias albispecularis* | Grey-headed Robin | | * | * | 4 | | | 3 | 3 | 3 |

| Family | Species | Common | NCR | END | VIS | Abund. Index | Sites | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | C1 | C2 | P1 | P2 | P3 |
| Petroicidae | *Tregellasia capito* | Pale-yellow Robin | | | * | 3 | | | 1 | 3 | 1 |
| Pachycephalidae | *Colluricincla boweri* | Bowers Shrike-Thrush | | * | * | 2 | | | | 1 | 2 |
| Pachycephalidae | *Colluricincla megarhyncha* | Little Shrike-Thrush | | | | 4 | | | 3 | 3 | 3 |
| Pachycephalidae | *Pachycephala pectoralis* | Golden Whistler | | | | 1 | | | | 1 | 1 |
| Pachycephalidae | *Pachycephala simplex* | Grey Whistler | | | | 3 | | | 1 | 2 | 3 |
| Climacteridae | *Cormobates leucophaeus* | White-throated Treecreeper | | | | 3 | | | 2 | 2 | 3 |
| Dicaeidae | *Dicaeum hirundinaceum* | Mistletoebird | | | | 1 | | | | 1 | |
| Zosteropidae | *Zosterops lateralis* | Silvereye | | | | 1 | | | | | 1 |
| Meliphagidae | *Lichenostomus frenatus* | Bridled Honeyeater | | * | * | 4 | 1 | | 3 | 3 | 3 |
| Meliphagidae | *Meliphaga lewinii* | Lewin's Honeyeater | | | | 3 | | | 2 | 3 | 3 |
| Meliphagidae | *Meliphaga notata* | Yellow-spotted Honeyeater | | | | 3 | | | 2 | 3 | 2 |
| Meliphagidae | *Myzomela obscura* | Dusky Honeyeater | | | | 2 | | | 1 | 1 | 1 |
| Meliphagidae | *Xanthotis macleayana* | Macleay's Honeyeater | | * | * | 3 | | | 2 | 3 | 3 |
| Sturnidae | *Aplonis metallica* | Metallic starling | | | | 2 | 10+ | | | | |
| Artamidae | *Strepera graculina* | Pied Currawong | | | | 2 | | | 2 | 1 | |
| Ptilonorhynchidae | *Ailuroedus melanotis* | Spotted Catbird | | | * | 3 | | | 2 | 3 | 3 |
| Ptilonorhynchidae | *Scenopoeetes dentirostris* | Tooth-billed Bowerbird | | * | * | 3 | | | 1 | 3 | 2 |
| Paradisaeidae | *Ptiloris victoriae* | Victoria's Riflebird | | * | * | 3 | | | 3 | 3 | 3 |
| | | | | | | | | | | | |
| Chelidae | *Elseya latisternum* | Sawshell Tortoise | | | | 3 | 3 | 3 | | | |
| Gekkonidae | *Carphodactylus laevis* | Chameleon Gecko | | * | * | 1 | | | 1 | | |
| Gekkonidae | *Saltuarius cornutus* | Northern Leaf-tailed Gecko | | * | * | 1 | | | | 1 | 1 |
| Scincidae | *Carlia rubrigularis* | Northern Red-throated Skink | | * | * | 4 | 6 | 3 | 3 | 11 | 15 |
| Scincidae | *Egernia frerei* | Major Skink | | | | 1 | | | 1 | | |
| Scincidae | *Eulamprus quoyii* | Eastern Water Skink | | | | 3 | 2 | 2 | | | |
| Scincidae | *Eulamprus tigrinus* | | R | * | * | 2 | | | 1 | | 3 |
| Scincidae | *Gnypetoscincus queenslandiae* | Prickly Forest Skink | | * | * | 4 | 1 | 1 | 3 | 8 | 27 |
| Scincidae | *Lampropholis coggeri* | | | * | * | 3 | 1 | | 5 | 5 | 12 |
| Scincidae | *Saproscincus basiliscus* | | | * | * | 4 | 1 | 1 | 16 | 18 | 10 |
| Scincidae | *Saproscincus tetradactyla* | Four-toed Litter Skink | | * | * | 3 | 1 | 1 | 3 | 1 | 5 |
| Agamidae | *Hypsilurus boydii* | Boyd's Forest Dragon | | * | * | 1 | | | 1 | | 1 |
| Agamidae | *Physignathus lesueurii* | Eastern Water Dragon | | | | 4 | 31 | 4 | | | |
| Varanidae | *Varanus scalaris* | | | | | 1 | | | 1 | | 1 |
| Typhlopidae | *Ramphotyphlops polygrammicus* | | | | | 1 | | | 1 | | |
| Boidae | *Morelia amethestina* | Amethystine Python | | | | 1 | | | 2 | | |
| Boidae | *Morelia spilota* | Carpet Python | | | | 2 | | | 1 | | 2 |
| Colubridae | *Dendrelaphis calligastra* | Northern Tree Snake | | | | 1 | | | 1 | | |
| Colubridae | *Dendrolaphis punctulata* | Common Tree Snake | | | | 2 | 1 | 1 | | | |

| Family | Species | Common | NCR | END | VIS | Abund. Index | Sites | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | C1 | C2 | P1 | P2 | P3 |
| Colubridae | *Tropidonophis mairii* | Keelback | | | | 1 | 1 | | | | |
| Elapidae | *Pseudechis porphyriacus* | Red-bellied Black Snake | | | | 2 | 1 | 1 | 1 | | |
| Elapidae | *Rhinoplocephalus nigrescens* | Eastern Smalleyed Snake | | | | 2 | | | | 1 | 1 |
| Bufonidae | *Bufo marinus* | Cane Toad | | | | 2 | | | | 3 | |
| Hylidae | *Litoria genimaculata* | Green-eyed Treefrog | R | | * | 3 | 31 | 1 | | | |
| Hylidae | *Litoria lesueuri* | Stony-creek Frog | | | | 3 | 23 | 1 | 2 | | |
| Hylidae | *Litoria nannotis* | Waterfall Frog | E | * | * | 3 | 16 | 5 | | | |
| Hylidae | *Litoria rheocola* | Common Mistfrog | E | * | * | 3 | 50+ | 2 | | | |
| Microhylidae | *Cophixalus infacetus* | Buzzing Nursery-Frog | R | * | * | 2 | | 4 | 1 | | |
| Microhylidae | *Cophixalus ornatus* | Common Nursery-Frog | | * | * | 3 | | 2 | 2 | | |
| Microhylidae | *Sphenophryne pluvialis* | White-browed Chirper | | * | * | 2 | | 2 | 1 | | |
| Microhylidae | *Sphenophryne robusta* | Pealing Chirper | R | * | * | 2 | | 1 | 1 | 1 | |
| Myobatrachidae | *Mixophyes schevilli* | Northern Barred-Frog | | * | * | 1 | | 1 | | | |

# CALCAREA FROM THE GREAT BARRIER REEF. 1: CRYPTIC CALCINEA FROM HERON ISLAND AND WISTARI REEF (CAPRICORN-BUNKER GROUP)

GERT WÖRHEIDE AND JOHN N.A. HOOPER

Wörheide, G. & Hooper, J.N.A. 1999 06 30: Calcarea from the Great Barrier Reef. 1: Cryptic Calcinea from Heron Island and Wistari Reef (Capricorn-Bunker Group). *Memoirs of the Queensland Museum* **43**(2): 859-891. Brisbane. ISSN 0079-8835.

Fourteen species of calcareous sponges (Porifera: Calcarea) of the subclass Calcinea are described from cryptic and semi-cryptic habitats of Heron Island and Wistari Reef, Capricorn-Bunker Group, southern Great Barrier Reef (GBR). Three are new records for the GBR (*Soleniscus stolonifer* (Dendy, 1891); *Leucaltis clathria* Haeckel, 1872; *Leucetta microraphis* Haeckel, 1872), one a new locality record for Australia (*Levinella prolifera* (Dendy, 1913)), and eight are new to science (*Clathrina heronensis*, *C. wistariensis*, *C. adusta*, *C. parva*, *C. helveola*, *C. luteoculcitella*, *Soleniscus radovani* and *Leucetta villosa* n. spp.). In the taxonomically difficult groups *Clathrina* and *Leucetta* differentiation between sibling species is supported by statistically significant differences in actinal lengths of spicules. Stable isotope analysis of spicules from nine species in both subclasses of Calcarea show a clear distinction between Calcinea (negative $^{13}C$ values) and Calcaronea (positive $^{13}C$ values), indicating that different biocalcification processes might take place in each subclass. ❐ *Porifera, Calcarea, Calcinea, Clathrina, Soleniscus, Levinella, Leucaltis, Leucetta, Pericharax, taxonomy, new species, Great Barrier Reef.*

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Calcarea, or calcareous sponges (Phylum Porifera), have an exclusively calcium carbonate spicule skeleton, clearly differentiating them from the other two poriferan classes Demospongiae and Hexactinellida (with spicules composed of silica). Calcareous sponges have persisted since the early Cambrian, with little apparent morphological divergence, and some (the 'Pharetronids') have contributed significantly to reef-building throughout different periods of the Earth's history (Reitner, 1992). Molecular data show that calcareous sponges might be the link between lower and higher metazoan phyla (Ctenophora/Cnidaria) (Lafay et al., 1992; Cavalier-Smith et al., 1996; van de Peer & de Wachter, 1997) and Calcarea show a unique composition in their skeleton and histological features compared to the other classes: only in Calcarea are all three stages of development of the aquiferous system realised (asconoid-syconoid-leuconoid).

Modern Calcarea are now mostly found hidden in cryptic habitats (e.g. caves, overhangs, coral rubble). This might be explained by early divergence in evolutionary strategies between Demospongiae and Calcarea, expressed by a lower level of chemical activity in calcarean secondary metabolites, as compared to demosponges (van Soest & Braekman, 1999). Cryptic habitats provide a large surface area and different environmental conditions within reef systems, and the highly diverse but so far virtually undescribed sponge fauna (Demospongiae, Calcarea) is one of the main constituents of the sessile macro-benthos within this vast cryptic reef system.

Knowledge of Recent Calcarea worldwide is substantially poorer than for other groups of Porifera, given their relatively poor fossil record, their difficult taxonomy and cryptic life style, and that the state of identification for most of calcarean collections is still relatively rudimentary. In contrast to tropical reefs, Calcarea are relatively well known from temperate Australian waters since the late 1800's (e.g. Carter, 1886; Dendy, 1891, 1892a,b), whereas the tropical fauna has only been investigated relatively haphazardly (e.g. Poléjaeff, 1883; Lendenfeld, 1885a,b; Burton, 1934; Pulitzer-Finali, 1982). It is hypothesised that this latter fauna comprises a vast, relatively unexplored resource. Moreover, existing collections of Calcarea were usually obtained by indirect sampling methods (e.g. dredging), with no data on habitat, ecology or community structure. These existing collections are largely badly preserved, and therefore their descriptions often lack any proper documentation or graphical depiction of cellular and

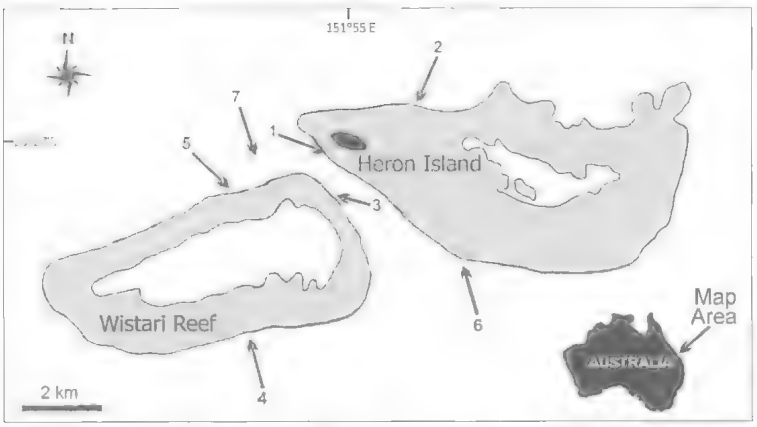



FIG. 1. Sites sampled at Wistari Reef and Heron Island, S GBR. 1, Underside of coral rubble, reef crest of Heron Island at Wistari Channel; 2, Tenements, N side of Heron Island; overhangs under coral bommies; 3, Wistari Reef, E side of Wistari Channel; steep wall with small overhangs; 4, Wistari Reef, S side; small patch reefs with overhangs; 5, Wistari Reef, N side; shallow bommies near reef crest with swim-throughs and overhangs; 6, Heron Island, S side near Wistari Channel; small crevices under bommies; 7, 'The Patch', between Heron Island and Wistari Reef, N of Wistari Channel, overhangs in cemented coral rubble.

skeletal features. These shortcomings are pertinent to our present understanding of calcarean biodiversity throughout Australasia.

Taxonomy of Calcarea is based on a combination of characters obtained from detailed studies of growth form, structure of the aquiferous system, architecture of soft tissue, larval development, cytological characters (e.g. position of the nucleus in choanocytes), morphology and association of calcareous spicules, and their specific arrangement within the soft tissue — features which are difficult or impossible to discern in poorly preserved collections. This makes the examination and documentation of contemporary samples, using a variety of methods, mandatory (e.g. spicule preparations, histological sections, ultra-thin sections for TEM), involving several different procedures for fixation, subsequent preservation, post-fixation, and histological preparation for examination in the laboratory. In this project emphasis was placed on specialised fixation techniques using a variety of methods, to allow subsequent multidisciplinary studies (e.g. light microscopy, SEM, TEM, molecular genetics, biogeochemistry, geochemistry). This present contribution provides a careful and detailed initial taxonomic investigation of GBR Calcarea, as a sound basis for further detailed studies.

This publication is the first comprehensive taxonomic study of Calcarea in Australasia in over 50 years. It documents calcarean biodiversity from cryptic and non-cryptic habitats of the southern Great Barrier Reef. So far only 14 species have been described for the entire GBR (see Hooper & Wiedenmayer, 1994). By comparison, there are now over 1,500 species of Demospongiae collected from the GBR, housed in the collections of the Queensland Museum (Hooper, pers. com.), of which only 428 have been described so far in scientific literature (Hooper & Wiedenmayer, 1994). Present results demonstrate that calcinean Calcarea are highly diverse in cryptic- and semi-cryptic habitats of the S GBR, with 70% of species collected new to science. A second contribution will describe the Calcaronea from this region, with subsequent publications documenting Calcarea from the northern and central sections of the GBR (Wörheide, in prep.).

Since the early works of Haeckel (1872) and Dendy & Row (1913), the supra-specific classification of Calcarea has been a topic of continuous discussion (e.g. Hartman, 1958, 1982; Burton, 1963; Borojévic et al., 1990, in press). The present study follows the supra-specific classification of Borojévic et al. (1990) for Calcinea.

## MATERIAL AND METHODS

COLLECTION. Samples of Calcarea were collected from Heron Island and Wistari Reef, S GBR (Fig. 1), from a variety of habitats, using SCUBA, under GBRMPA Permit nos. G98/142 and G98/022.

For each sample collected the depth and habitat were recorded using protocols developed by Wörheide (1998) (Fig. 2). Where possible, underwater photographs of all samples were taken, although this was not always feasible given that most cryptic Calcarea are very small and dwell in small crevices and other cryptic habitats where photography is not possible. Consequently, samples were also photographed

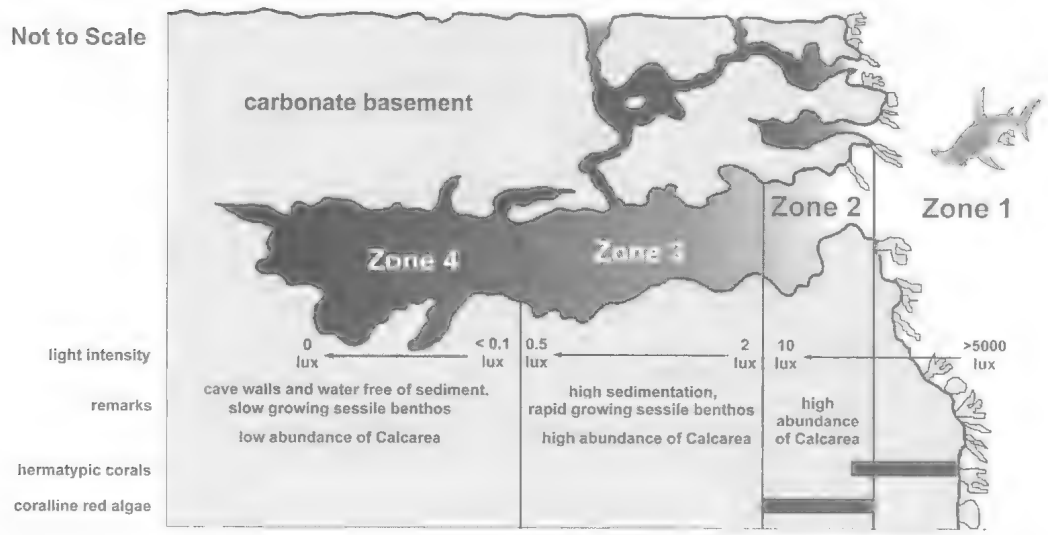



FIG. 2. Schematic model of reef cave zonation, noting the occurrence of Calcarea, habitat characteristics, light regimes, and associated biota (modified from Wörheide, 1998).

post-fixation at the Queensland Museum using a macro-lens camera set-up.

FIXATION OF SPECIMENS. Specimens were fixed shortly after collection, using a variety of methods (depending on purpose of study). In addition to fixation for routine taxonomic identification (see below), subsamples of each specimen were fixed and/or preserved for molecular biology (DNA analysis; Wörheide, 1998) and electron microscopy (TEM/SEM) (Willenz & Hartman, 1989; Wörheide, 1998).

*Fixation for histological thick sections and spicule preparations.* Samples were fixed for 24hrs in a 4% Glutaraldehyde/sterile filtered seawater solution, buffered with 0.2M sodium cacodylate, supplemented with 0.35M sucrose. After fixation, samples were rinsed three times with unbuffered sterile filtered seawater. Samples were then transferred through a graded EtOH-series and stored in 70% EtOH. At least one large piece of tissue from all specimens collected was treated in this way to ensure proper fixation for subsequent staining, essential to make tissue sections for routine taxonomic identification.

Two standard preparations were applied to each sample for taxonomic identification.

HISTOLOGY. Detailed methods are presented here as these protocols have not been published previously.

*Spicule preparations.* Descriptions of spicules were made from different regions of the sponge body (e.g. osculum, cortex, atrium), in addition to skeletal architecture, spicule dimensions, and associations between spicules from different regions of the body.

For spicule preparations, small pieces of soft tissue were cut and dissolved in sodium hypochlorite. After complete digestion of the soft tissue the solution was drained and the supernatant washed three times each in distilled water and absolute ethanol. Spicules were then transferred onto microscopic slides and embedded in Canada Balsam. Unused portions of spicule preparations were kept in absolute alcohol for subsequent bio-/geochemical investigations (e.g. stable isotopes, see below).

*Sections of sponge tissue.* It is mandatory to prepare good anatomical sections of soft tissue and spicules, as Calcarea often show a complex differential distribution of skeletal structures between the cortex, choanosome and/ or central atrial tube. Tissue was stained using acid Fuchsin, and hand sections were made using a scalpel after embedding one or more fragments of sponge in paraffin (after Borojevic, pers. com.). Good sections were obtained mostly in cross-section, allowing examination of skeletal organisation of the cortical, choanosomal and atrial regions. Sections were made at variable thickness depending on the species under examination and the size of their spicules.

Thinner sections are desirable in order to investigate the arrangement of choanocytes within the choanosome, and to recognise details of spicule distributions, whereas thicker sections are essential to reveal relationships among different spicule elements within the sponge wall.

The following protocol was used to prepare sections of the sponge body. Samples were kept in 70% ethanol prior to sectioning. Selected parts of the sponge body containing cortical, choanosomal, and atrial regions (if present), were cut using a scalpel prior to dehydrating. Preparation times given below apply to tissue blocks of $1cm^3$ maximum volume, whereas most tissue samples were smaller than this.

*Dehydrating and staining.* Tissue was stained in a saturated solution of acid Fuchsin in 70% EtOH for 60mins; washed three times in 70% EtOH (30mins each); transferred to 90% EtOH (30mins); and two changes of absolute EtOH (30mins each).

*Clearing.* Tissue was transferred two times into xylene (30mins each).

*Infiltration.* Tissue was transferred to a mixture of xylene and melted paraffin wax (1:1) in an oven (60°C) for 60mins and two changes of melted paraffin wax in an oven (60°C) (60mins each).

*Embedding.* Selected moulds were lightly coated with glycerol, enabling solidified paraffin blocks to be easily removed, and moulds filled with molten paraffin wax; tissue placed in wax using warmed forceps and arranged in the correct plane for sectioning (preferably in cross-section allowing cutting of the cortex, choanosome and atrium); when the wax block was partially set (i.e. with a thin scum appearing over the surface of the block), blocks were placed in the refrigerator to ensure rapid cooling and to prevent crystallisation of the wax.

*Sectioning.* After paraffin had hardened, blocks were released from the mould and trimmed with a scalpel to the desired size and cutting plane; sections of different thickness were cut by hand with a scalpel.

*De-paraffinisation.* Sections were placed on a microscope slide on a hot plate to allow the paraffin to partially melt again, and thus flattening sections (sections normally curl after sectioning). Excess paraffin was soaked up with paper tissue. Slides were removed from the hot plate to cool and re-harden. Slides were de-paraffinised in two changes of xylene (15mins each).

*Mounting.* After all paraffin was removed, sections were mounted using Durcupan embedding resin (ACM Fluka) and covered with a cover-glass.

Spicule preparations and tissue sections were examined using an Olympus BH-2 Stereomicroscope equipped with a Panasonic WV-CP410 digital camera and a Snappy video grabber (Play Inc.), providing digital photographs with a resolution of up to 300dpi, a maximum size of 1500 ×1125 pixels, and 24-bit color depth. Measurements were made using a calibrated scale and camera lucida and are presented as range of minimum-(mean)-maximum length × minimum-(mean)-maximum width, in µm (n=30, or as indicated). Statistical analyses were performed using 'Origin 3.0' (MicroCal).

All type material was deposited in the collections of the Queensland Museum, Brisbane. Abbreviations: AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London;GBR, Great Barrier Reef, Qld., Australia; NMV, Museum of Victoria, Melbourne; PMJ, Phyletisches Museum, Jena; Qld., Queensland; QM, Queensland Museum, Brisbane.

STABLE ISOTOPE ANALYSIS OF CALCAREAN SPICULES. Small numbers (100-150µg) of spicules from unused portions of spicule preparations were used as bulk samples for analysis of $\delta^{18}O$ and $\delta^{13}C$ values. Measurements were made on a Finnigan MAT 252 with automated Kiel carbonate device using '100%' phosphoric acid at 75°C. Data were corrected for $^{17}O$ interferenee using the method of Santrock et al. (1985) and are reported in permille relative to PDB (Peedee belemnite).

## RESULTS

FIELD OBSERVATIONS. Abundanee and diversity of Calcarea from cryptic habitats around Heron Island and Wistari Reef was surprisingly high given the few species recorded so far in the literature. Although these reefs contain no known deep caves (i.e. with restricted light regimes, and thus containing a distinct suite of fauna), a large number of specimens were collected from semi-cryptic habitats such as overhangs, small crevices, and swim-throughs (Zones 1-3; Fig. 2). Patchy species distributions were notable, with some species abundant at certain sites but absent elsewhere on the reef. For example, *Solenlscus radovani* sp. nov., was only found at one site on the S side of Wistari Reef.

where it was the most dominant calcareous sponge, but so far not recorded at any of the other sites. Whether these patchy distributions are the result of species adaptations to specialised niche requirements, or a random effect due to haphazard larval settlement etc., cannot be resolved from present data. Generally, however, small and fragile Calcarea appear to be most common in semi-dark/dark and sheltered habitats, whereas more massive species, such as *Pericharax heteroraphis* and *Leucetta chagosensis*, are more abundant in fully illuminated parts of the reef.

Similar patchy species distributions were observed on reefs around Lizard I. and the outer barrier reefs (Ribbon Reef #10, Yonge Reef), with different species dominant at different sites. In this region of the GBR there are several large caves with a distinct zonation of species related to light regimes. Although our data are still preliminary, the calcarean fauna of the N GBR, around Lizard I., differs from the fauna of the S GBR, around Heron I. (Wörheide, unpublished data). This observation supports the findings of Hooper et al. (1999), that the GBR demosponge fauna has distinct latitudinal gradients in species diversity and composition, although more substantial taxonomic studies are required to substantiate this claim for Calcarea.

## SYSTEMATICS

Fourteen species of Calcarea (Subclass Calcinea, Order Clathrinida) are described here, from five families and six genera (following the scheme of Borojévic et al., 1990), of which eight are new species, three are new records for the GBR and one new for the Australian fauna. Diagnoses of Calcinea higher taxa follow Borojevic et al. (1990) and Borojevic & Klautau (in press).

### Class **Calcarea** Bowerbank, 1864

Exclusively marine Porifera in which the mineral skeleton is composed entirely of calcium carbonate. Spicules are diactines, triactines and tetractines. Calcarea are always viviparous.

### Subclass **Calcinea** Bidder, 1898

Calcarea with regular (equiangular and equiactinal), or exceptionally parasagittal or sagittal triactines, and a basal system of tetractines. In terms of ontogeny, triactines are the first spicules to be secreted. Choanocytes are basinucleate with spherical nuclei. The basal body of the flagellum is not adjacent to the nucleus. Calcinea incubate coeloblastula larvae.

### Order **Clathrinida** Hartman, 1958

Calcinea with skeleton composed exclusively of free spicules, without hypercalcified non-spicular tracts, calcareous scales, or plates.

### Family **Clathrinidae** Minchin, 1900

Clathrinidae with an essentially tubular organisation. A continuous choanoderm lines all the internal cavities. Growth is by longitudinal median divisions and anastomosis of tubes to form large units, called the cormus. There is neither a common cortex nor a well-defined inhalant or exhalant aquiferous system.

#### **Clathrina** Gray, 1867

*Clathrina* Gray, 1867: 557.
*Ascetta* Haeckel, 1872: 14; Dendy & Row, 1913: 788.
*Ascaltis* Haeckel, 1872: 51; Dendy & Row, 1913: 787.
*Leucopsis* Lendenfeld, 1885b: 1089.

Clathrinidae in which the choanoderm is flat, or rarely raised into conuli, by the apical actines of large tetractines, but never forming true folds, at least when the sponge is in the extended state. The cormus is composed of anastomosed tubes. The skeleton contains regular, equiangular and equiradiate triactines and/or tetractines, to which diactines or tripods may be added.

#### **Clathrina heronensis** sp. nov.
(Fig. 3A-F, Table 1)

ETYMOLOGY. For the type locality.

MATERIAL. HOLOTYPE: QMG313647, Heron I., at Wistari Channel, GBR, 23°26.9'S, 151°54.6'E, opposite Research Station, 300m S of shipping channel, at reef crest, 21.vi.1998, coll. G. Wörheide (reef-walking).

HABITAT AND DISTRIBUTION. Under rubble on reef crest, intertidal. Heron I., S GBR.

DESCRIPTION. *Growth form*. Mass of loosely anastomosing tubes, approximately 1mm diameter, with fairly large spaces between tubes, cormus 3×2cm, flat.

*Colour*. White in life, brownish after fixation with Glutaraldehyde in EtOH.

*Oscules*. Macroscopically not visible; no distinct exhalant system visible.

*Texture*. Soft, compressible, delicate.

*Surface ornamentation*. Smooth.

*Ectosomal skeleton*. No ectosome/cortex

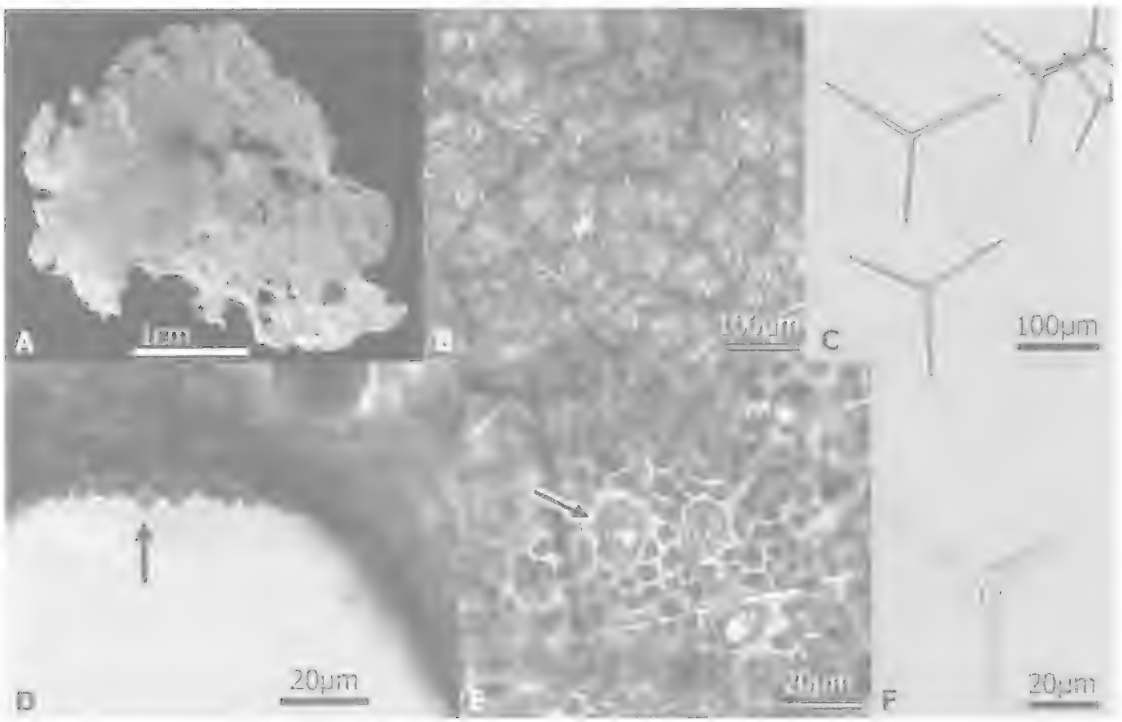



FIG. 3. *Clathrina heronensis* sp. nov. (holotype QMG313647). A, holotype after fixation. B, wall of a tube with irregularly arranged triactines. C, cylindrical triactines. D, cross-section of one tube showing choanocytes (arrow) continuously lining the tube wall. E, magnification of tube wall with ostiae (in porocytes, arrow) and surrounding choanocytes. F, small, actively growing triactine with conical actines.

distinguishable.

*Choanosomal skeleton*. Irregular layer of triactines, with a mean thickness of 20-30µm. Triactines are tangentially orientated and their actines sometimes overlap, so that a few triactines (mostly not more than three) are stacked above each other. Sometimes the actines of larger triactines are aligned in a parallel pattern (one actine of one triactine is parallel to one actine of a second triactine), but mostly they are arranged irregularly, and are densely packed next to each other. No differentiation or zonation in the skeleton was observed, and the skeleton appears to be uniform throughout the cormus.

*Aquiferous system*. No defined inhalant or exhalant system is present. The water system has an asconoid grade of construction, with choanocytes continuously lining the internal walls of the tubes.

*Soft tissue*. The choanoderm has a dense appearance. Choanocytes continuously line the walls of tubes in 'circles' with porocytes in the center. Porocytes contain many granules with a brownish colour (in Fuchsin-stained sections), densely arranged around the small ostiae (1-3µm diameter). Choanocytes have a diameter of 2-3µm and a triangular to hexagonal shape in section parallel to the surface, and 2-5 are located between the porocytes (Fig. 3E). Porocytes have a diameter of 12-20µm in section parallel to the surface.

*Spicules*. The spicular skeleton consists of only one type of triactines, with no differentiation and/or zonation of spicules in different parts of the skeleton observed. Regular cylindrical triactines possess a more-or-less blunt tip with their actines measuring 84-(107)-126×8-(10)-12µm. A few pointed triactines, with more conical actines (30-70µm long), occur irregularly scattered throughout the skeleton, representing young, growing spicules. See Table 1 for statistics on triactine dimensions.

**Clathrina wistariensis** sp. nov.
(Fig. 4A-C, Table 1)

ETYMOLOGY. For the type locality.

MATERIAL. HOLOTYPE:. QMG313663, S side of

Wistari Reef, GBR, 23°29.4'S, 151°52.8'E, small reef patches, 18m depth, 07.vii.1998, coll. G. Wörheide (SCUBA).

HABITAT AND DISTRIBUTION. Under overhangs of small coral patches, Zone 2 (Fig. 2), 18m, Wistari Reef, S GBR.

DESCRIPTION. *Growth form*. Dense mass of anastomosing tubes, 1-2mm diameter, no large space between tubes, cormus 2×3cm, flat, attached to a calcareous hydrozoan.

*Colour*. White in life, brownish after fixation with Glutaraldehyde in EtOH.

*Oscules*. No oscules visible macroscopically.

*Texture*. Soft, easily torn.

*Surface ornamentation*. Smooth.

*Ectosomal skeleton*. Not distinguishable.

*Choanosomal skeleton*. Irregular layer of triactines, less than 20µm thick. Triactines are tangentially orientated, but not densely packed, with some space between their actines. Their actines sometimes overlap, so that a few triactines (mostly not more than three) are stacked above each other. Only occasionally are actines of larger triactines aligned in a parallel pattern (one actine of one triactine is parallel to one actine of a second triactine). Mostly they are irregularly arranged. No differentiation or zonation in the skeleton was observed, which appears to be predominantly uniform throughout the cormus.

*Aquiferous system*. No defined inhalant or exhalant system is present. The water system has an asconoid grade of construction.

*Soft tissue*. The choanoderm is light in appearance. Choanocytes continuously line the walls of tubes with porocytes in between. Sometimes there is a 'circular' arrangement of choanocytes around the porocytes, but more often choanocytes are clustered together. Porocytes contain few small granules with a brownish colour (in Fuchsin-stained sections), densely arranged around the large ostiae (up to 48µm diameter), in one layer only. Porocytes are up to 50µm diameter (with only one layer of granules), in section parallel to the surface. Granule-containing cells (size of 15-20µm diameter), which are either contracted porocytes or storage cells, are scattered in the choanoderm. Choanocytes have a mean diameter of 2µm and have predominantly a circular shape in section parallel to the surface.

*Spicules*. The spicular skeleton consists of only one type of triactine, with no differentiation and/or zonation of spicules between different parts of the skeleton. The majority of triactines (actines: 150-(175.16)-230×10-(13.7)-20µm), are regular and possess cylindrical actines with a more-or-less blunt tip; few triactines are slightly parasagittal (angles between actines are equal, but one actine is slightly shorter). Smaller triactines, with more conical actines, are also found, representing young, growing triactines. See Table 1 for statistics on triactine dimensions.

**Clathrina adusta** sp. nov.
(Fig. 4D-H; Table 1)

ETYMOLOGY. For the post-fixation brown coloration (Latin, *adustus*).

MATERIAL. HOLOTYPE: QMG313665: S side of Wistari Reef, GBR, 23°29.4'S, 151°52.8'E, 18m depth, 07.vii.1998, coll. G. Wörheide (SCUBA).

HABITAT AND DISTRIBUTION. Under overhangs of small coral patches, 18m depth, Zone 2 (Fig. 2). Specimen was overgrowing a calcareous hydrozoan. Wistari Reef, S GBR.

DESCRIPTION. *Growth form*. Dense mass of anastomosing tubes with small tubes (0.5mm diameter). Tubes fused together to form fewer, larger (excurrent) tubes (2-3mm diameter), which end in a terminal osculum. The cormus measures 2×2cm.

*Colour*. White in life, dark brown after fixation in Glutaraldehyde in EtOH.

*Oscules*. Few, on top of larger excurrent tubes.

*Texture*. Relatively firm, harsh.

*Surface ornamentation*. Smooth.

*Ectosomal skeleton*. Not differentiated.

*Choanosomal skeleton*. Sustained by a densely packed irregular layer of tangential triactines and tangentially orientated basal plane of tetractines (same size as triactines), forming the wall of tubes. Apical free actines of the tetractines protrude free into tubes. Actines of both triactines and the basal plane of tetractines are arranged without any order, although sometimes actines are aligned in parallel, but this seems to be random. Actines overlap so that few (not more than five) are stacked above each other. The tube walls have a thickness of up to 40µm. Tetractines are concentrated mostly in the walls of the larger (excurrent) tubes, with fewer present in the walls of smaller tubes.

*Aquiferous system*. With an asconoid grade of construction, where choanocytes continuously line the internal wall of tubes. Slightly larger excurrent canals do not represent a true atrium,

but are sometimes devoid of choanocytes in their distal parts (showing here only spherical cells with granules).

*Soft tissue.* The choanoderm appears dense. Choanocytes continuously line the walls of tubes, except in some of the distal parts of the larger excurrent canals. Choanocytes are arranged without any apparent order, sub-spherical and small, with a diameter of about 2µm in section parallel to the surface. Larger, brownish cells with granules are far more obvious, up to 15µm diameter. These cells occur in large numbers in all parts of the soft tissue, and are sometimes, in the distal parts of the larger tubes, the only visible cell type present. Whether these cells are contracted porocytes (no ostiae were visible in sections), a type of storage cell, or an early larval stage, cannot be determined with certainty without higher resolution microscopy.

*Spicules.* The major part of the skeleton consists of regular triactines with more-or-less cylindrical actines, with a size of 90-(108.13)-142× 12-(14.3)-20µm. The distal part of their actines is sometimes slightly undulated. A few tetractines are present, more abundant in the walls of the larger tubes. These tetractines possess a basal system of the same size as the triactines, with their reduced (thinner and shorter) free apical actine protruding into water canals. Neither triactines nor tetractines are arranged in any apparent order in any part of the skeleton. See Table 1 for statistics on triactine dimensions.

**Clathrina parva** sp. nov.
(Fig. 4I-K, Table 1)

ETYMOLOGY. For the small size of this species (Latin, *parvus*, little).

MATERIAL. HOLOTYPE: QMG313666, S side of Wistari Reef, GBR, 23°29.4'S, 151°52.8'E, 18m depth, 07.vii.1998, coll. G. Wörheide (SCUBA).

HABITAT AND DISTRIBUTION. Under overhangs of small coral patches, 18m depth, Zone 2 (Fig. 2), growing on a bryozoan. Wistari Reef, S GBR.

DESCRIPTION. *Growth form.* Small anastomosing tubes, with cormus <1×1cm in size.

*Colour.* White in life and after fixation in Glutaraldehyde in EtOH.

*Oscules.* A few prominent naked oscules are visible on the top of fused tubes.

*Texture.* Soft.

*Surface ornamentation.* Smooth.

*Ectosomal skeleton.* Not present.

*Choanosomal skeleton.* Irregular layer of triactines, about 15µm thick. Triactines are orientated tangentially, but not densely packed, with some space between the actines. Actines sometimes overlap, so that a few triactines (mostly not more than three) are stacked above each other. Only occasionally are actines of the larger triactines arranged in a parallel pattern (one actine of one triactine is aligned parallel to one actine of a second triactine), whereas mostly they are irregularly arranged. No differentiation or zonation in the skeleton was observed, which appears to be uniform throughout the cormus.

*Aquiferous system.* No well-defined inhalant or exhalant system present. The water system has an asconoid grade of construction, with choanocytes continuously lining the internal walls of tubes.

*Soft tissue.* The choanoderm is light in appearance. Choanocytes continuously line the walls of tubes, with porocytes in between, but are randomly arranged around porocytes, not in circles. Porocytes contain few small granules with a brownish colour (in Fuchsin-stained sections), densely arranged around ostiae (up to 15µm diameter), in only one layer. Porocytes are up to 25µm diameter (with a few layers of granules) in section parallel to the surface. Choanocytes have a mean diameter of 2-3µm and are predominantly circular in shape, parallel to the surface.

*Spicules.* The spicular skeleton consists of regular cylindrical triactines (actines: 80-(143)-185×10-(13.7)-20µm), with a more-or-less blunt tip, arranged without any apparent order. No zonation and/or differentiation was observed within the cormus. Some triactines are parasagittal (angles between actines equal, but one actine slightly shorter). Many smaller triactines, with more conical actines, were also found, representing young, growing triactines. See Table 1 for statistics on triactine dimensions.

**Clathrina helveola** sp. nov.
(Fig. 4L-N, Table 1)

ETYMOLOGY. For the pale yellow live coloration (Latin, *helveolus*).

MATERIAL. HOLOTYPE: QMG313680, S side of Heron I., GBR, 23°28.2'S, 151°56.7'E, 17m depth, 08.vii.1998, coll. G. Wörheide (SCUBA). PARATYPE: QMG313805, same locality.

HABITAT AND DISTRIBUTION. Overhangs, under coral bommies, Zone 2 (Fig. 2), 17m depth. Heron I., S GBR.

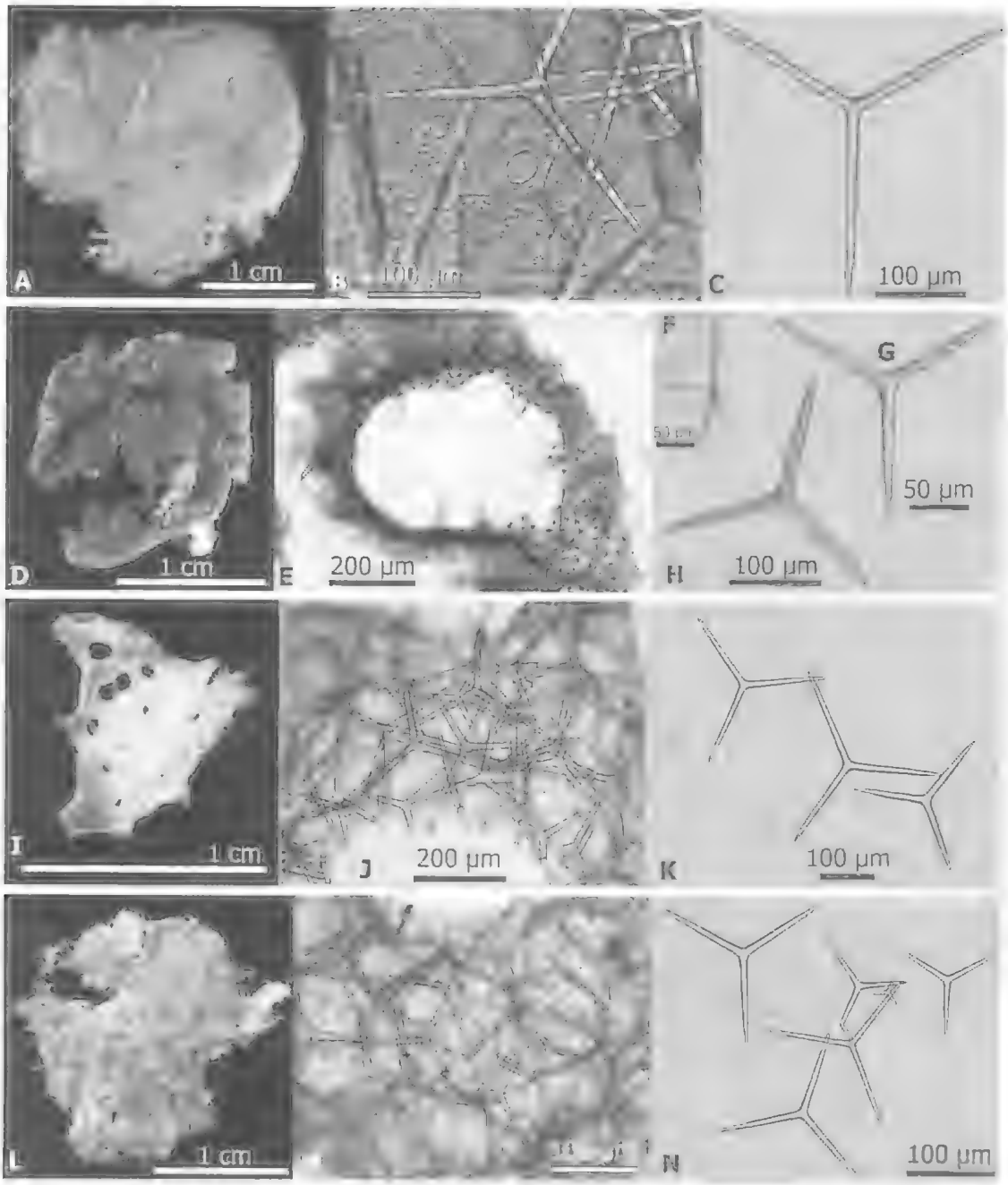



FIG. 4. *Clathrina* spp. A-C, *Clathrina wistariensis* sp. nov. (holotype QMG313663). A, holotype after fixation. B, section of tube wall. C, cylindrical triactine. D-H, *Clathrina adusta* sp. nov. (holotype QMG313665). D, holotype after fixation. E, cross section of tube wall with free actines of tetractines protruding into the tube. F, tetractine showing reduced free actine. G, triactine. H, basal system of tetractine. I-K, *Clathrina parva* sp. nov. (holotype QMG313666). I, holotype after fixation. J, section of tube wall. K, cylindrical triactines. L-N, *Clathrina helveola* sp. nov. (holotype QMG313680). L, holotype after fixation. M, section of tube wall. N, cylindrical triactines.

TABLE 1. Statistical comparisons between common forms of triactines in *Clathrina heronensis*, *C. wistariensis*, *C. adusta*, *C. parva*, *C. helveola* and *C. luteoculcitella* n.spp. Measurements in µm (n=30).

| | *C. heronensis* | | *C. wistariensis* | | *C. adusta* | | *C. parva* | | *C. helveola* | | *C. luteoculcitella* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Length | Width | Length | Width | Length | Width | Length | Width | Length | Width | Length | Width |
| Mean | 107 | 10 | 175.16 | 13.70 | 108.13 | 14.13 | 143 | 13.7 | 159.6 | 16.3 | 77.7 | 9.4 |
| St Dev. | 12.1 | 1.39 | 16.48 | 2.83 | 14.26 | 2.03 | 21 | 2.23 | 20.9 | 1.8 | 4.5 | 1.2 |
| Min. | 84 | 8 | 150 | 10.00 | 90 | 12 | 80 | 10 | 114 | 14 | 68 | 8 |
| Max. | 126 | 12 | 230 | 20.00 | 142 | 20 | 185 | 20 | 200 | 20 | 84 | 12 |

DESCRIPTION. *Growth form.* Mass of anastomosing tubes, each about 1mm diameter; dense cormus with some space between tubes (<2mm), cushion shaped, 2×3cm.

*Colour.* Yellowish in life, beige after fixation in Glutaraldehyde and in EtOH.

*Oscules.* None visible macroscopically.

*Texture.* Soft.

*Surface ornamentation.* Smooth.

*Ectosomal skeleton.* Not present.

*Choanosomal skeleton.* Tangential layer of triactines, irregularly orientated, forming walls of tubes. No differentiation and/or zonation was observed within the skeleton, with the skeleton uniform throughout the cormus. Actines of the tangentially orientated triactines sometimes overlap, so that a few triactines appear to be stacked above each other, but not more than five. Tube walls are 20-40µm thick. Only rarely are the actines of triactines aligned parallel to each other, in which case they form sub-hexagonal to hexagonal patterns. Triactines are not densely arranged in the tube wall.

*Aquiferous system.* The water system has an asconoid grade of construction, with choanocytes continuously lining internal walls of tubes. No well-defined inhalant or exhalant system present.

*Soft tissue.* The choanoderm is light in appearance, with cells appearing to be loosely arranged. Small choanocytes (3-4µm diameter), continuously line walls of tubes, without any apparent order, and only a few porocytes are present. Small spherical, sometimes granular, cells or bodies, twice the size of choanocytes, are scattered in large numbers in the soft tissue. Determination of the true nature of these cellular bodies requires TEM examination (in progress).

*Spicules.* The spicular skeleton consists only of one type of regular cylindrical triactines (actines: 114-(159.6)-200×14-(16.3)-20µm), with no zonation and/or differentiation within the cormus observed. Actines of the triactines are sometimes slightly undulated in their distal part and some possess blunt tips. A few triactines show a bent tip on one of their actines (Fig. 4N). Numerous smaller triactines, with more conical actines and sharp, pointed tips, are irregularly scattered between larger triactines. These small triactines are young, growing spicules.

### **Clathrina luteoculcitella** sp. nov.
(Fig. 5A-E, Table 1)

ETYMOLOGY. For the yellow color and pillow-like shape of the cormus (Latin, *luteus*, yellow; *culcitella*, pillow).

MATERIAL. HOLOTYPE: QMG313684, 'The Patch', at the N end of the channel between Heron I. and Wistari Reef, GBR, 23°26.6'S, 151°53.4'E, 25m depth, 09.vii.1998, coll. G. Wörheide (SCUBA). PARATYPE: QMG313806, same locality.

HABITAT AND DISTRIBUTION. Overhangs in boulders of cemented coral rubble, Zone 3 (Fig. 3), 25m depth. Heron I., S GBR.

DESCRIPTION. *Growth form.* Dense mass of small anastomosing tubes, each with diameter of about 0.5mm, cushion shaped, with only little space between the tubes (<1mm).

*Colour.* Yellow in life, yellow-beige after fixation in Glutaraldehyde in EtOH.

*Oscules.* No oscules visible macroscopically.

*Texture.* Soft.

*Surface ornamentation.* Smooth.

*Ectosomal skeleton.* No defined ectosomal skeleton, but diactines are found in some areas perpendicular to, and protruding through, the walls of tubes.

*Choanosomal skeleton.* Irregular tangential layer of triactines, build the walls of tubes. Tube walls are 20-30µm thick. Triactines are not really densely packed but do overlap with their actines, so that not more than five triactines are partially stacked above each other to form the tube walls. No differentiation and/or zonation of triactines was observed. Diactines are present in some areas of the cormus, perpendicular to the tube

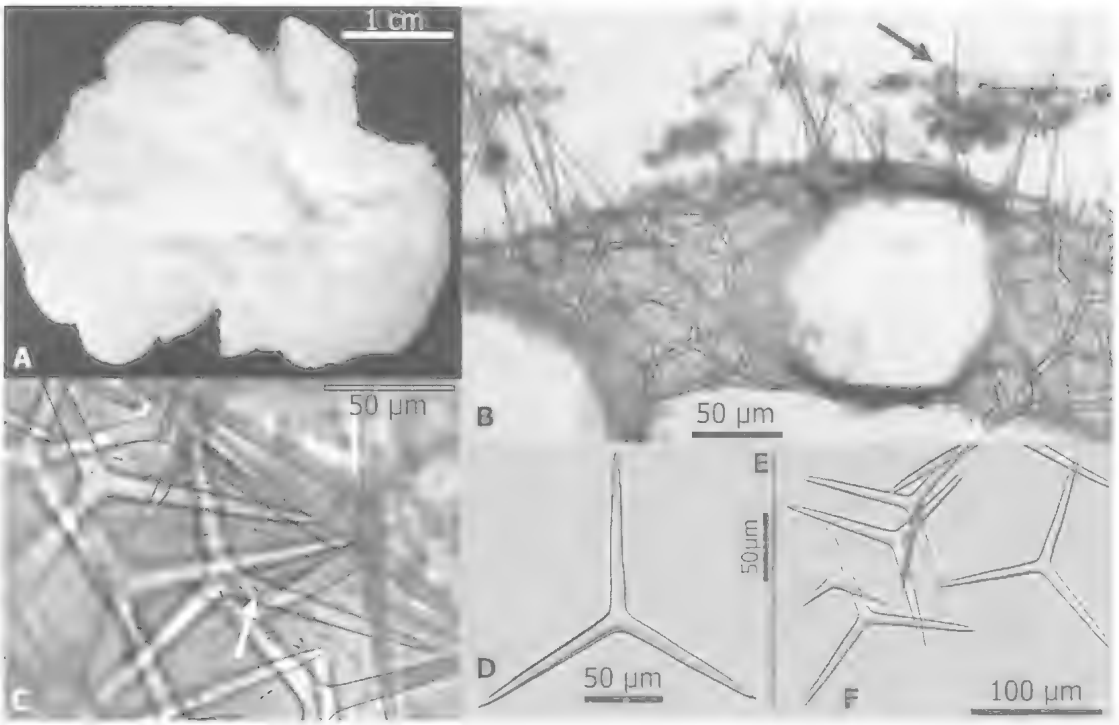



FIG. 5. *Clathrina luteoculcitella* sp. nov. (Holotype QMG313684). A, holotype after fixation. B, cross-section through tube wall with perpendicular diactines (arrow). C, section of tube wall with irregularly arranged triactines and bacteria in the tissue (arrow). D, cylindrical triactine with blunt tips. E, diactine. F, two sizes of triactines.

wall. These diactines protrude through the tube wall with their thicker proximal bases slightly protruding into the tube. Their sharply pointed, thinner distal end sometimes baffles and holds fine grained sediment (Fig. 5B). Diactines are numerous at the external surface of the cormus, but are also found in some areas within the cormus, on the external surfaces of larger tubes, although no distinct pattern of localisation was recognised.

*Aquiferous system*. With an asconoid grade of construction, with choanocytes continuously lining all internal tube walls. No defined inhalant or exhalant system present.

*Soft tissue*. The choanoderm has a dense appearance. Subspherical choanocytes, 3-4µm diameter, are arranged without any order or pattern side-by-side, with only few gaps between. Neither porocytes nor granular cells were observed, but rod-like bacteria (possibly cyanobacteria) are rarely present in the soft tissue (Fig. 5C).

*Spicules*. The spicular skeleton consists of regular, cylindrical triactines of a single size (actines: 68-(77.7)-84×8-(9.4)-12µm), with distal end of actines slightly undulated (Fig. 5D), and diactines (90-(164.4)-220×2-(3.12)-6µm). Diactines have one thin, sharply pointed end (distal) and one thicker, blunt end (proximal). Additionally, a few smaller, conical triactines were found, representing young, growing spicules. No zonation and/or differentiation of triactines was observed. Diactines are concentrated in the external surface but are also found within cavities of the cormus on the external surfaces of tubes.

## REMARKS ON *CLATHRINA*

Classification of *Clathrina* is very difficult (Borojevic & Boury-Esnault, 1987), given that most species have only few morphological characters useful for taxonomy (e.g. only a single type of triactine). Studies on Atlantic populations of *Clathrina*, using biochemical and molecular approaches (Solé-Cava et al., 1991; Klautau et al., 1994), showed that very small morphological differences correspond to quite large genetic differences, representing genetically distinct

species. These authors showed that complete genetic separation of sympatric and allopatric populations of *Clathrina* was linked to very small or sometimes undetectable differences in 'classical' taxonomic characters. Taxonomy, based exclusively on these 'classical' morphological characters, appears to be overconservative. Many 'regional species' or populations previously classified as being simple varieties of so-called 'cosmopolitan species', therefore most likely represent distinct taxa. In contrast, Wörheide (1998) demonstrated using molecular approaches (RFLP of rDNA), that geometric differences in spicule morphology of the reef cave-dwelling, ultraconservative, coralline demosponge *Astrosclera willeyana* (with the genus *Astrosclera* present at least since the Triassic; Wörheide, 1998), do not appear to correspond to a genetic separation of allopatric populations across the Indo-Pacific (Red Sea to Fiji). Whether this observation is also valid for other (modern) demosponge or calcarean sponge groups has yet to be tested. Further studies are in progress (see below). For the current classification of *Clathrina* from the GBR, the results of Solé-Cava et al. (1991) and Klautau et al. (1994) are adopted here, with empirical support provided by statistical comparisons of spicule dimensions (Table 1).

Haeckel's (1872) original description of *C. primordialis* is vague concerning the dimensions of spicules (i.e. only one type of triactines, ranging from 100-200µm in length), with nearly the same dimensions recorded for *C. coriacea* (60-120µm, depending on the geographic variety). However, *C. primordialis* is well differentiated from *C. coriacea* by the different shape of actines of the triactines (conical versus cylindrical, respectively; see Haeckel, 1872, Plate 5, Figs 1-2). Haeckel (1872: 22) also noted the high variability in spicule size of *C. primordialis* from different parts of the world, and described several generic and specific varieties based on differences in cormus-shape and spicule size. Haeckel also mentioned an Australian variety with very large spicules (180-200µm length), without naming the variety. Unfortunately he did not describe the type locality for *C. primordialis* or its varieties, nor for *C. coriacea*. After more detailed comparative studies, Borojevic (1971) subsequently designated La Manche (British Channel), as the type locality for *C. coriacea*, and Klautau et al. (1994) nominated Rio de Janeiro (Brazil) as the type locality for *C. primordialis*. Although some species from the GBR show general affinities to both *C. coriacea* and *C. primordialis* (based on the shape of their triactinal actines), these species are described as new taxa, given: 1) the high improbability that *Clathrina* species from the GBR are conspecific with taxa from the North or South Atlantic; and 2) all new species of *Clathrina* described here from the S GBR differ consistently in one or more characters despite their geographic sympatric distribution. Using light microscopy and thick-sectioning (the latter technique essential for determining skeletal structure), it was possible to ascertain that each of these species differed slightly in their cytological features, as judged by the density of choanocytes, patterns of choanocyte arrangement, presence/absence of granular cells, occurrence, size and shape of porocytes. However, more sophisticated, thin- and ultra-sectioning techniques are required to accurately describe and identify the different cell types in each of these species.

*Clathrina* spp. are also supposedly readily contractile, largely influenced by local environmental conditions (as first observed many years ago by Haeckel, 1872, for *C. clathrus*). Consequently, it is possible that certain cytological features may be altered after fixation (i.e. cell contraction) (Borojevic pers. comm.). It is likely, therefore, that tube wall dimensions may not be an accurate mensural character to differentiate between these alied species, given that this feature is the most likely gross feature to expand and contract in response to local hydrodynamic conditions. More detailed studies on the cell biology and ultrastructure of the soft tissue, using electron microscopy (SEM/TEM), are currently in progress, seeking to answer some of these cytological questions, and to evaluate the use of cytological features as potential taxonomic tools (Wörheide, in prep.).

Statistical analyses of triactine dimensions were compared between species. For species with only one type of spicule (viz. *C. heronensis*, *C. wistariensis*, *C. helveola* and *C. parva*), this is currently the only consistent 'classical' feature to differentiate species. Pairwise-comparisons between spicule actinal-lengths in each species were made using a Student t-test at a confidence level of 99%. This analysis showed consistent and significant differences in spicule lengths between all species ($t=2.663$, $P<0.01$, $n=30$), supporting their recognition as distinct taxa. *Clathrina adusta* and *C. luteoculcitella* also possess a second type of spicule (tetractines and diactines, respectively), making it easy to

differentiate them from the other GBR *Clathrina*. Based on illustrations of Haeckel (1872: Plate 5, Figs 1-2), the shape of actines of triactinal spicules in *C. heronensis*, *C. wistariensis*, *C. parva* and *C. helveola* show superficial similarities to those of *C. coriacea*, having a characteristic cylindrical shape and more-or-less blunt triactine tips. On this basis these species are referred to as members of the 'coriacea-group'.

Yellow *Clathrina* are have been identified as: *C. clathrus*, described by Schmidt (1864) from the Mediterranean (with relatively small triactines; 92×5.5µm; Borojevic & Klautau, in press); *C. aurea*, described by Sole-Cava et al. (1992) from the Atlantic (with even smaller triactines; 72×5.6µm); or more recently as *C. chrysea*, described by Borojevic & Klautau (in press) from New Caledonia (with longer actines; 105×9.8µm). By comparison, *C. helveola* from the GBR has much larger triactines than these three species (with a mean 159.6×16.3µm, n=30), which is distinctive amongst all species. To support the current species classification, additional studies on molecular genetics and systematics of other Indo-Pacific *Clathrina* are in progress, with expectations that results will hopefully clarify questions of species boundaries within this difficult genus, and eventually supporting or refuting the utility of statistical differences in spicule size, as proposed here, to differentiate GBR *Clathrina* spp.

Family **Soleniscidae** Borojevic et al., 1990

Clathrinida with an essentially tubular organisation, growing in the form of an individual olynthus, with several olynthi growing from the basal stolon-like tubes or in the form of distally ramified tubes radially arranged around a central olynthus tube, without any special skeletal differentiation. A continuous choanoderm lines all the internal cavities. Spicules are regular triactines and/or tetractines, to which tripods or diactines may be added.

**Soleniscus** Borojevic et al., 1990

'*Soleniscus*', 'generic variety' of Haeckel, 1869: 244.
*Soleniscus* Borojevic et al., 1990:253.

Soleniscidae in the form of an individual olynthus, with several olynthi growing from basal stolon-like tubes, or in the form of distally ramified creeping tubes.

REMARKS. Even though *Soleniscus* has been attributed by authors to Haeckel (1869), Borojevic et al. (1990) correctly note that Haeckel never formally attributed this name at the generic level, but merely mentioned it as a 'generic variety'. Consequently, *Soleniscus* must be attributed to Borojevic et al. (1990).

**Soleniscus radovani** sp. nov.
(Fig. 6A-H)

ETYMOLOGY. For Radovan Borojevic, in recognition of his substantial and pioneering achievements in calcarean taxonomy.

MATERIAL. HOLOTYPE: QMG313661, S side of Wistari Reef, GBR, 23°29.4'S, 151°52.8'E, 17m depth, 07.vii.1998, coll. G. Wörheide (SCUBA). PARATYPE: QMG313807, same locality.

HABITAT AND DISTRIBUTION. Small patches of coral, under overhangs, Zone 2 (Fig. 2), 17m depth. Wistari Reef, S GBR.

DESCRIPTION. *Growth form.* Aborescent, bushy, with single, delicate tubes branching dichotomously and polychotomously from a few central tubes. The central, proximal tube is larger than distal tubes, and tubes ramify only in the lower part of the sponge 'bush'. Distal parts of the tubes are mostly longer than the ramified parts. Bushy, single tubes are approximately 2mm diameter. Two tubes sometimes fuse together at their distal end, just below the osculum. Size of the sponge 'bush' is <5cm.

*Colour.* Bright yellow in life, brownish-beige after fixation in Glutaraldehyde in EtOH.

*Oscules.* One naked osculum occurs on top of each tube, with slightly smaller diameter than the tube itself. When two tubes are fused together, one osculum is located at the distal end of the fused tubes, just above their point of fusion.

*Texture.* Soft, delicate, easily torn.

*Surface ornamentation.* Smooth.

*Ectosomal skeleton.* Not present.

*Choanosomal skeleton.* The skeleton consists only of sagittal tetractines. Tangentially arranged, parasagittal facial plane of the tetractines forms the wall of tubes, with one (the longer) ray of the basal triradiate system pointing in the direction of the growth axis (i.e. directed towards the central tube). Actines of tetractines overlap, with no more than three stacked above each other to form the tube wall, 15-20µm thick. The curved, free actines of tetractines protrude into the tube, and sometimes a 'tent' like tissue was observed over the tips of the free actines inside the tube (Fig. 6F). Tips of free actines are bent in the

direction of the osculum. No zonation and/or differentiation of tetractines was observed within tubes.

*Aquiferous system.* Asconoid grade of construction, with choanocytes continuously lining walls of the tubes. The (single) tubes grow in the form of an individual olynthus and several distally ramified olynthi tubes grow radially arranged around a central olynthus tube, with a terminal osculum on top of each tube. No single central atrium is present.

*Soft tissue.* The choanoderm has a dense appearance. Choanocytes 4-6µm diameter, and partially clustered and partially arranged in circles of 2-3 choanocytes surrounding small ostiae (<2µm diameter), which are not always visible in the center of circles in thick sections. Choanocytes are subspherical to hexagonal in section parallel to the surface, and are basinucleate (with the nucleus at the base of the choanocyte).

*Spicules.* Only one spicule type is present, consisting of sagittal tetractines with a curved apical actine. No differentiation and/or zonation of spicules was observed within tubes. Basal triradiate system is predominantly parasagittal, with slightly curved paired actines and one longer unpaired basipetal actine. The apical actine is bent at the tip ('whipped'), and is either slightly enlarged or reduced. The non-curved longer unpaired actine of the basal triradiate system measures 120-(152)-190µm×8-(10)-12µm (n=10), and the paired shorter (curved) actines of the pseudosagittal basal plane measure 85-(111)-130×8-(10)-12µm (n=10).

REMARKS. *Soleniscus radovani* is most similar to *S. (Ascilla) japonica* (Haeckel, 1872) from California, although in *S. japonica* all three actines of the basal system are equal. In *S. radovani* the basipetal actine is longer than the other two actines, which is regarded here as a distinctive character to differentiate these species.

**Soleniscus stolonifer** (Dendy, 1891)
(Fig. 6G-O)

*Leucosolenia stolonifer* Dendy, 1891: 46, pl. i, fig. 2; pl. vi, figs 1-3; pl. ix, fig. 2; Dendy & Row, 1913: 723; Dendy, 1924: 275; Tanita, 1942: 81; Burton, 1963: 182.
*Soleniscus stolonifer*; Borojevic et al., 1990: 253.

MATERIAL. LECTOTYPE: BMNH1891.9.19.4 (Dendy collection), near Port Phillip Heads, Victoria, coll. J.B. Wilson. OTHER MATERIAL: QMG313668, N side of Wistari Reef, GBR, 23°27.2'S, 151°53.2'E, 5m depth, 07.vii.1998, coll. G. Wörheide (SCUBA).

HABITAT AND DISTRIBUTION. Shallow swimthroughs between coral bommies, Zone 2 (Fig. 2), 5m depth. Port Phillip Heads (Victoria) and S GBR (Qld); New Zealand.

DESCRIPTION. Growth form. Several olynthus-like tubes grow from basal stolon-like tubes. Distal tubes ramify and the proximal (deeper and older) tubes are larger (0.5cm diameter) than the distal (top) tubes, which are slightly conical (>1mm at the osculum). The size of the specimen is 2×3cm.

*Colour.* White in life, beige after fixation in Glutaraldehyde in EtOH.

*Oscules.* One naked osculum is apical at the end of each distal tube.

*Texture.* Smooth.

*Surface ornamentation.* No surface ornamentation is visible macroscopically, but fine grained silt and organic material produces a dirty-whitish cover (like dust) on the external surface of tubes.

*Ectosomal skeleton.* Diactines are arranged perpendicular to the surface of tubes in 'tee-pee'-like bundles, where individual diactines are aligned at an angle of <45° to each other and cross in their proximal lower third. These diactines are covered with a biofilm which contains small sediment particles, diatoms, and foraminiferans (producing the 'dusty' appearance on the external surface). The slightly broader base of diactines sometimes protrudes slightly through the choanosomal skeleton, whereas the proximal part of diactines is mostly anchored between the basal systems of the tetractines, not protruding into the tube.

*Choanosomal skeleton.* The choanosomal skeleton is sustained by a tangentially arranged basal triradiate system of tetractines of very variable size and form, forming the walls of tubes. Two main types of spicules were distinguished: a larger regular, and a smaller parasagittal-sagittal type of tetractine. Their apical actines, which are sometimes greatly exaggerated in the larger regular type, and reduced in the smaller sagittal type, protrude into the tube. Actines of their basal triradiate systems, which are thicker in the regular type, do overlap, with up to five actines partially stacked above each other, supporting the tube wall. Tube walls have a thickness of about 100µm (excluding the diactines). No differentiation and/or zonation of spicule types was observed.

*Aquiferous system.* This species has an asconoid grade of construction with choanocytes continuously lining the walls of tubes. Tubes grow in the form of an individual olynthus from

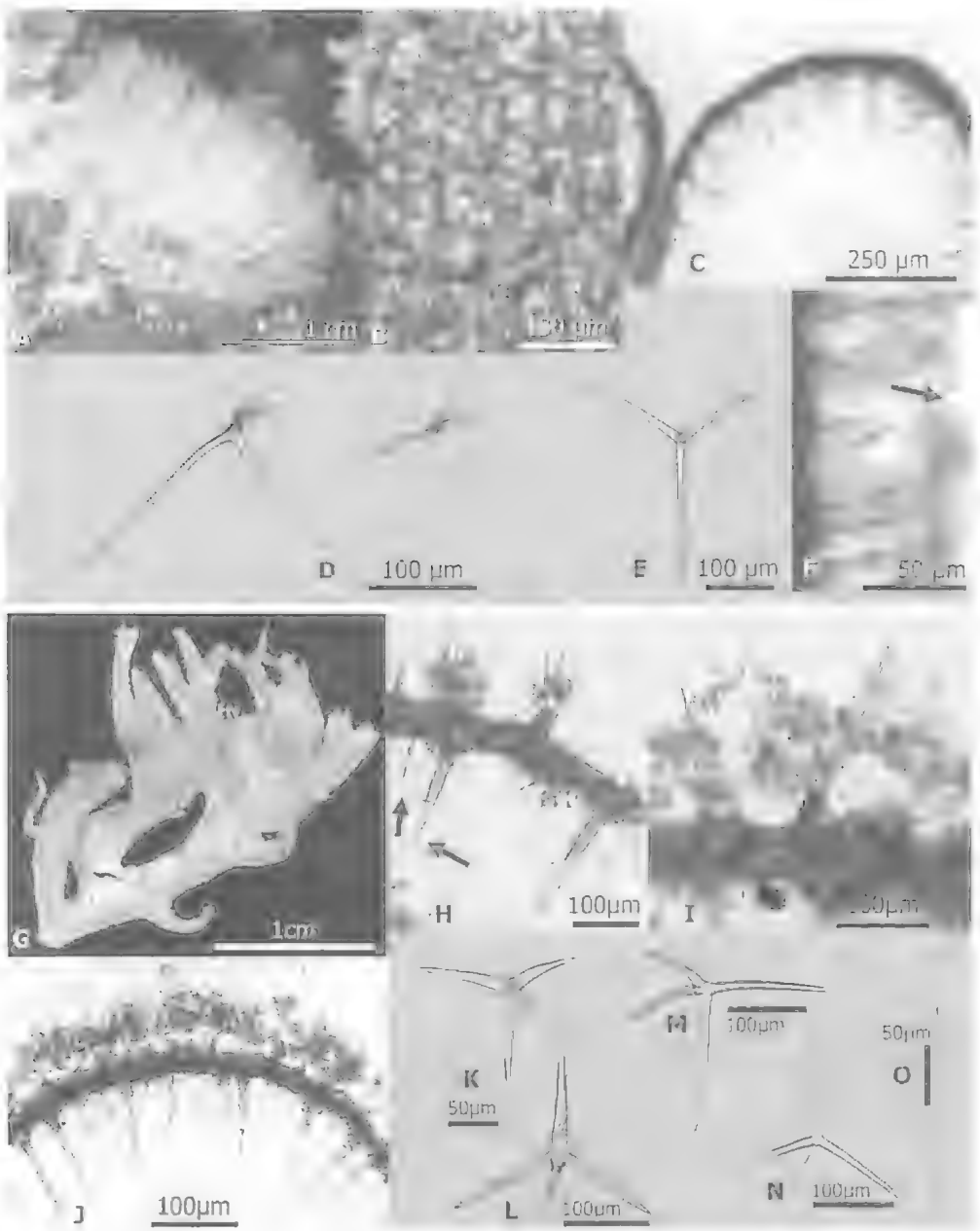



FIG. 6. *Soleniscus* spp. A-H, *Soleniscus radovani* sp. nov. (holotype QMG313661, histological sections and spicules; paratype QMG313807, *in situ* photograph). A, paratype in situ from Wistari Reef. B, section of tube wall with basal system of sagittal tetractines, longer unpaired actines point towards central tube (bottom of image). C, Cross section of one tube with free actines of sagittal tetractines protruding into the tube. D, two sagittal tetractines with curved free actine and longer unpaired actine of basal system. E, basal system of sagittal tetractine with longer unpaired actine. F, cross section of tube with bent free actines and 'tent-like' tissue over their tips. The tips of the free actines are bent in the direction of the osculum (top of image). G-O, *Soleniscus stolonifer* (Dendy, 1891) (specimen QMG313668). G, specimen after fixation. H, cross-section of tube wall showing two sizes of free actines of tetractines building the skeleton of the wall (arrows) (compare with K,N in this figure). I, cross-section of tube wall showing 'tee-pee' like bundled diactines with baffled sediment particles. J, cross-section of tube wall. K, regular tetractine. L, regular tetractine. M, sagittal tetractine with curved free actine. N, tetractine with reduced 'whip-like' apical actine. O, diactine.

the basal stolon-like tube, with a terminal osculum on top of each tube.

*Soft tissue.* A dense choanoderm covers the internal walls of tubes, which are continuously lined by choanocytes. The choanoderm also covers the lower 10-15% of the proximal part of the free actines of regular larger tetractines, protruding into the tube. Distal parts of these free actines are partly covered with cells, but not with choanocytes, as are the smaller, 'whip-like', free actines of smaller sagittal tetractines. Choanocytes are basinucleate (i.e. with the nucleus at the base of the cell), measuring 4-7µm diameter, and possessing a long flagellum (up to three times the size of the choanocyte). Open spaces within the skeleton, between the choanoderm and external surface (built by the basal triradiate systems of tetractine spicules), is filled with a mesohyle of yet unknown cellular composition. This mesohyl is certainly free of choanocytes and contains some archaeocytes. Ectosomal exopinacoderm covers the basal triradiate systems of choanosomal tetractines on the external surface. The 'tee-pee'-like bundles of ectosomal diactines are also covered in their lower parts, up to their last point of crossing, with exopinacoderm. Ostiae (<10µm diameter) are scattered on the external surface between the bundles of diactines.

*Spicules.* Regular tetractines with conical actines, sharply pointed, 80-(129.9)-170× 8-(12.2)-21µm, sometimes with an exaggerated apical actine (up to 500µm) (n=25); parasagittal to sagittal tetractines with mostly reduced apical actines, length of shorter paired actines 40-(81.6)-110µm, length of longer unpaired actine 80-(124.4)-160µm, width of actines 8-(9.7)-12µm (n=25); diactines 150-(207.8)-260×4-(5.7)-8µm, sometimes sinused, with one broader part near the proximal end, but both tips sharply pointed, fusiform (n=25).

REMARKS. This is the first record of the species for the GBR. It was initially described by Dendy (1891) as a species of *Leucosolenia* (Calcaronea) from Port Phillip Heads (Victoria), and was later described by Dendy (1924) from New Zealand. However, the species clearly belongs to Calcinea due to its possession of basinucleolate choanocytes (see Dendy, 1891: plate 6, fig. 2), which were also observed in the specimen described here. This species is the types species of *Soleniscus*, as stated by Borojevic et al. (1990), because of its characteristic morphological features (several olynthi arising from basal, stolon-like tubes; its spicule types; asconoid grade of construction; and basinucleolate choanocytes). Although the growth form of the specimen described here (with a wider central tube and conical and thinner distal tubes), is slightly different from that described by Dendy (1891: pl. 1, fig. 2) (with thinner basal tube and wider cylindrical distal tubes), the spicular skeleton is very similar. Dendy (1891: 47) mentioned a large variability in both spicule size and spicule morphology in his specimens, but clearly recognised that the free apical actine of tetractines was sometimes exaggerated, which he regarded as typical and distinctive for this species. This feature was also observed in the specimen studied here. Dendy (1891) also noted, as typical for *S. stolonifer*, the peculiar form of the ectosomal diactines, often being slightly irregularly curved, with one broader proximal end but with both tips sharply pointed. The same form of diactines was observed in the specimen from the GBR, although the diactines observed here are only about half the size of the largest ones described by Dendy (1891) (which were up to 700µm long). Despite differences in spicule sizes (which Dendy suggested may vary greatly in this species), and differences in the growth form, this specimen from the GBR is assigned to *S. stolonifer* identical skeletal structure as described by Dendy (1891) (i.e. only two types of spicules present; some tetractines with exaggerated free apical actines; and peculiarly formed diactines), and the same organisation of the soft tissue (see Dendy, 1891: pl. 6, figs 1,3).

### Family **Levinellidae** Borojevic & Boury-Esnault, 1986

Clathrinida with a cormus composed of a central tube which may be ramified, and of diverticuli isolated or grouped in clusters. The skeleton of the central and radial tubes is composed of regular (equiactinal and equiangular), and/or parasagittal spicules. The skeleton of the diverticuli is composed of regular and/or parasagittal spicules, always clearly distinct from spicules which form the skeleton of the central tube. Differences occur in the size of spicules between the diverticuli and those of the central tube, where the latter the spicules are larger. The choanoderm either lines all the central cavity or is restricted to the diverticuli (emend.).

### **Levinella** Borojevic & Boury-Esnault, 1986

*Levinella* Borojevic & Boury-Esnault, 1986: 444; 1987: 22; Borojevic et al., 1990: 255.

Levinellidae with a cormus divided into a central

tube and external diverticuli. The central tube is not ramified. A choanoderm lines all the internal cavities.

**Levinella prolifera** (Dendy, 1913)
(Fig. 7A-H)

*Dendya prolifera* Dendy, 1913: 6, pl. i, figs 3-4; pl. iii, figs 4-5; Dendy & Row, 1913: 728; Burton, 1930: 2, figs 1-2; 1963: 232, text fig. 99.
*Levinella prolifera*; Borojevic & Boury-Esnault 1986: 447.

MATERIAL. HOLOTYPE: BMNH 1920.12.9.49, 'Sealark' Collection, Amirante Is. (Seychelles), 80m depth. OTHER MATERIAL: QMG313664, S side of Wistari Reef, 23°29.4'S, 151°52.8'E, 18m depth, 07.vii.1998, coll. S.D. Cook & G. Wörheide (SCUBA). Fragment sent to N. Boury-Esnault (Centre d'Océanologique de Marseille, Station marine d'Endoume, Marseille, France).

HABITAT AND DISTRIBUTION. Small patches of coral in 18m depth, under overhangs, Zone 2 (Fig. 2). Indian Ocean (Seychelles); Indonesia; S GBR (Qld, Australia).

DESCRIPTION. *Growth form.* The specimen has a size of about 2.5cm and consists of one central tube (4mm diameter) with clustered diverticuli around the central tube (<2mm size) extending to about 2mm below the osculum. The upper 2mm of the central tube is free of diverticuli.

*Colour.* Brownish-beige in life and after fixation in Glutaraldehyde in EtOH.

*Oscules.* One naked osculum at apical end of the central tube.

*Texture.* Soft.

*Surface ornamentation.* Clustered diverticuli around the central tube, resembling a 'bunch of grapes'.

*Ectosomal skeleton.* No distinct ectosomal skeleton.

*Choanosomal skeleton.* The central tube is not ramified and choanocytes sparsely line the walls of the central tube with distinct ostia between them (up to 40µm diameter). The density of choanocytes in this region is not as high as those in the diverticuli. The wall of the central tube, translucent in the upper part where no diverticuli are found, is sustained by tangential regular and parasagittal to sagittal triactines and the tangentially orientated regular and parasagittal basal system of tetractines, with not more than three overlapping actines forming the thin wall of the tube (thickness 30-50µm). Triactines and tetractines are arranged without any apparent order or direction, scattered irregularly in the wall of the central tube. Some free actines of the tetractines protrude into the tube. Fewer tetractines occur here as compared with those in the proximal parts of the diverticuli. Diverticuli ramify from the central tube into clusters of little tubes. They originate from one cavity/larger tube splitting from the central tube and ramify from this 'proximal diverticuli-tube/cavity'. This latter structure is sometimes developed as a small tube (250µm diameter), branching from the central tube, and sometimes like a bulbous, half spherical, 'chamber-like' extension of the central tube (up to 500µm diameter), from which up to ten other tubes of the diverticuli ramify. The walls of the diverticuli are supported by tangential regular and parasagittal to sagittal triactines and the parasagittal basal systems of tetractines. Two, or less often three overlapping actines form the walls of the diverticuli, 10-20µm thick. Many free actines of tetractines protrude into the 'proximal diverticuli tube', their number decreasing distally, and in the most distal parts of the ramified diverticuli tubes are devoid of free tetractinal actines. Distal parts of diverticuli are constructed by tangential parasagittal and sagittal triactines with their unpaired actines directed towards the distal end of diverticuli, away from the central tube.

*Aquiferous system.* A choanoderm lines all internal cavities of the sponge (central tube and diverticuli), and although the density of the choanoderm is reduced in the central tube, the central tube is not regarded as a true atrium, because numerous choanocytes are present (whereas the term 'atrium' is restricted to a central exhalant-only cavity, devoid of choanoderm). The aquiferous system has an asconoid grade of construction.

*Soft tissue.* The soft tissue of the central tube is thin, delicate, slightly translucent and cells are only sparsely present. Choanocytes, 4-6µm diameter, are sometimes clustered together or solitary, but not as densely arranged here as they are in the diverticuli. Their shape is sub-spherical to hexagonal in section parallel to the surface. Amoeboid archaeocytes were observed scattered between choanocytes, slightly smaller than choanocytes. The soft tissue of diverticuli appears to be denser than the soft tissue of the central tube. All walls of diverticuli are lined by choanocytes in rows of 1-3, surrounding the ostiae. Ostiae 10-20µm diameter. Choanocytes have a subspherical, pseudo-hexagonal to hexagonal shape and a size of 4-10µm in section parallel to the

surface. Rod-shaped bacteria (possibly cyanobacteria), 5-8µm long, are sometimes scattered in the soft tissue of diverticuli. Only few amoeboid archaeocytes are present in diverticuli.

*Spicules*. *Central tube*: regular triactines with cylindrical actines, 70-(110.4)-140×8-(9)-12µm (n=10); parasagittal equiangular triactines with cylindrical actines, longer unpaired actine 120-(229.2)-360×8-(10.64)-15µm, shorter paired actines (curved proximal) 80-(174.8)-290×8-(10.64)-15µm (n=25); parasagittal tetractines with reduced apical actine and cylindrical actines of the basal triradiate system, equiangular basal system similar to the parasagittal triactines, longer unpaired actine 120-(188.4)-290×8-(10.2)-12µm, shorter paired actines (curved proximal) of the basal system 85-(142.2)-190×8-(10.2)-12µm, apical actine reduced; few regular tetractines with cylindrical actines of the triradiate basal system, with curved apical actine, actines of the basal triradiate system 80-(112)-200×8-(9.2)-11µm (n=10). Diverticuli, regular cylindrical triactines 50- (74.2)-100×5-(7.5)-10µm (n=12); parasagittal to sometimes sagittal cylindrical triactines (about 10% are sagittal, e.g. enlarged unpaired angle), longer unpaired actine 70-(116.4)-160×5-(7.64)-10µm, shorter paired actines, mostly proximally slightly curved 60-(79.8)-100×5-(7.64)-10µm (n=25); parasagittal cylindrical tetractines with often reduced apical actine, longer unpaired actine 100-(125.41)-140×7-(8.75)-10µm, shorter paired actines, mostly proximally slightly curved 70-(90)-100×7-(8.75)-10µm (n=12), apical actine 40-(70)-90µm (n=3); rare regular cylindrical tetractines with a curved apical actine 50-(73.3)-100×5-(7.3)-9µm (n=3).

REMARKS. Initially described in *Dendya* (Dendy, 1913), with type locality from the Seychelles, Borojevic & Boury-Esnault (1986) referred it to their new genus *Levinella*, but without comprehensive redescription. *Dendya prolifera* was reported by Burton (1930) from Indonesia, whereas the specimen described here is the first record of this species for Australia. The specimen described by Dendy (1913) had a very characteristic and unique morphology, and the species is readily recognisable in the field, resembling a 'bunch of grapes'. Based on obvious similarities in skeletal features (size and form of spicules, arrangement of diverticuli around the central tube; see Dendy, 1913, pl. 3, fig. 4), the present material from the GBR is clearly conspecific with Dendy's (1913) species, and easily assigned to *Levinella prolifera*. However, in the definition of the genus *Levinella*, Borojevic et al. (1990: 254) described the skeleton of the central and radial tubes as composed of 'regular (equiradiate and equiangular) spicules', whereas this is neither the case in the holotype of *Levinella prolifera* (Dendy, 1913: 8; pl. 3, fig. 5a), nor in the specimen described here. In both specimens the skeleton of the central tube consists partly of parasagittal spicules (such as seen in the diverticuli). Differences in spicules between central tube and diverticuli are mainly in their size (spicules of the central tube are larger), and the definition of the family is emended here accordingly.

## Family **Leucaltidae** Dendy & Row, 1913

Clathrinida with tubular, ramified or anastomosed cormus bearing many osculae, or occurring in the form of single tubes each with a single large terminal osculum. The tubes have a large atrium surrounded by a strong wall composed of a distinct cortex and a choanosome. The cortical skeleton is composed of large tangential triactines and/or tetractines. The choanoskeleton may be absent, reduced to apical actines of cortical tetractines, or contains small and irregularly dispersed triactines and tetractines.

### **Leucaltis** Haeckel, 1872

*Leucaltis* Haeckel, 1872: 142; Dendy & Row, 1913: 737.
*Heteropegma* Polejaeff, 1883: 25, 45.

Leucaltidae with a body composed of large, ramified and anastomosed tubes. Each tube has a distinct strong cortex sustained by large triactines and tetractines. The choanosome is organised in elongate, radial chambers, which open to the central atrial cavity. It is supported by apical actines of cortical tetractines and small scattered triactines and tetractines.

### **Leucaltis clathria** Haeckel, 1872 (Fig. 7I-S)

*Leucaltis clathria* Haeckel, 1872: 159, pl. 26, fig. 3; Dendy & Row, 1913: 738; Dendy, 1913: 16, pl. 2, figs 1-2; Hozawa, 1940: 136, pl. 6, fig. 3; Arndt, 1940: 46; Tanita, 1943: 394, pl. 8, fig. 27; Borojevic & Peixinho, 1976: 1002, fig. 8; Borojevic & Klautau, in press.
*Heteropegma nodusgordii* Polejaeff, 1883: 45, pl. 1, fig. 7, pl. 4, fig 1.
*Leucaltis bathybia mascarenica* Ridley, 1884: 625, Pl. 54a,a'.
*Clathrina latimbulata* Carter, 1886: 515.
(see Burton, 1963: 549 for detailed synonymy)

MATERIAL. HOLOTYPE: Unknown; BMNH 1956.4.26.42 (slide) fragment of type. OTHER MATERIAL: QMG313676, S side of Heron I., GBR,

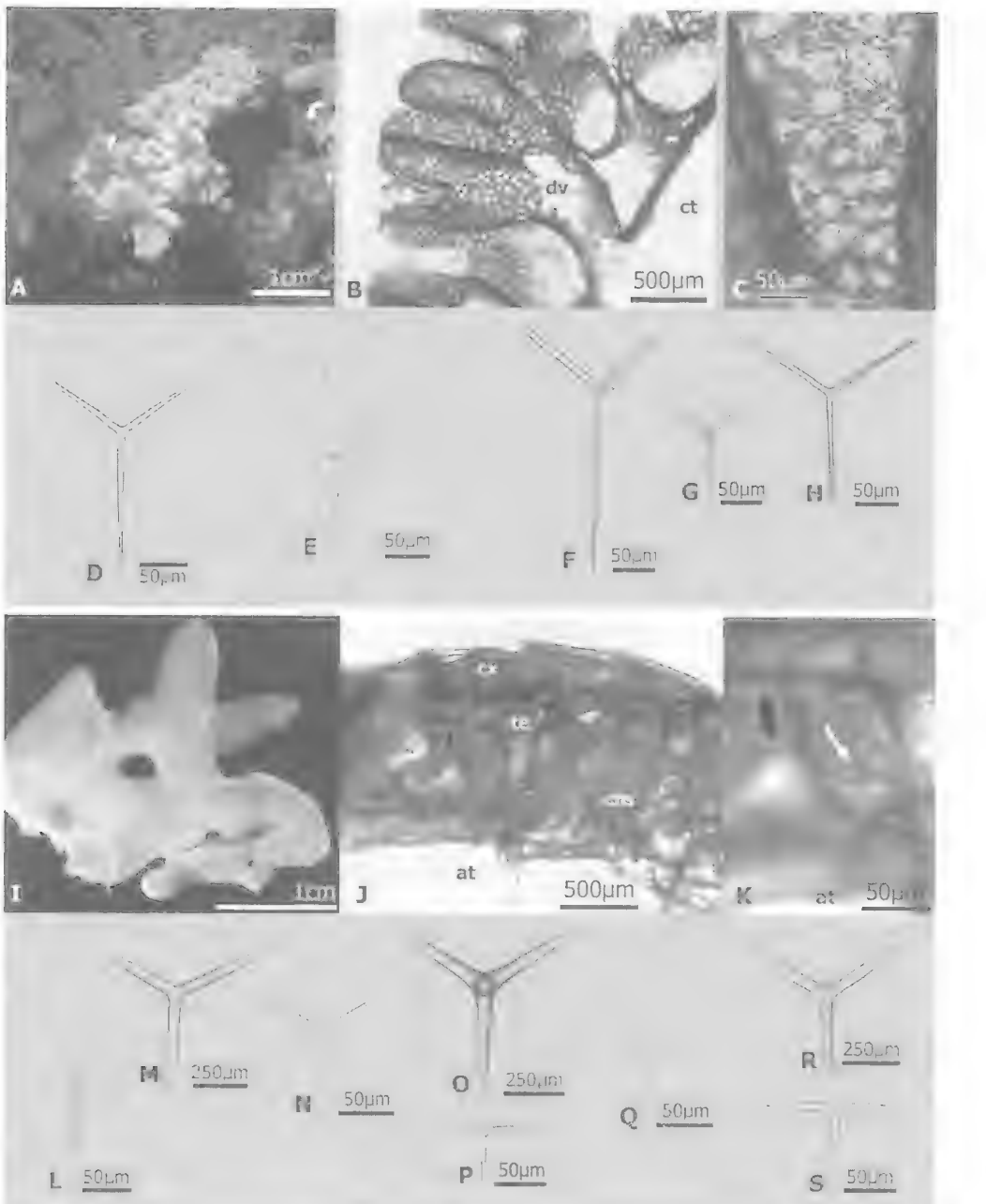



FIG. 7. *Levinella* and *Leucaltis* spp. A-H, *Levinella prolifera* (Dendy, 1913) (specimen QMG313664). A, specimen in situ. B, section through the diverticuli (dv) and part of the central tube (ct). C, section through one diverticuli with ostiae (round holes) and surrounding choanocytes. D, parasagittal triactine of the diverticuli. E, two parasagittal to sagittal triactines and one parasagittal tetractine (center) of the diverticuli. F, parasagittal tetractine of the central tube. G, small parasagittal tetractine of the central tube. H, regular triactine of the central tube. I-S, *Leucaltis clathria* Haeckel, 1872 (specimen QMG313676). I, specimen after fixation. J, cross-section through the tube wall with cortex (cx), choanosome (chs), atrium (at), and a large tetractine (te) which free apical actine protruding through the choanosome into the atrium. K, enlargement of the inner choanosome with triactine (arrow) atrial tetractine (at). L, atrial tetractine. M, cortical triactine., N, choanosomal tetractine. O, large subcortical tetractine. P, atrial tetractine. Q, choanosomal triactine. R, cortical triactine with one bent actine. S, atrial triactine.

23°28.2'S, 151°56.7'E, 08.vii.1998, 17m depth, coll. G. Wörheide (SCUBA).

HABITAT AND DISTRIBUTION. Small crevices under coral bommies in 17m water depth, Zone 2 (Fig. 2). Apparently cosmopolitan. Distribution in Australia: Houtman Abrolhos (Western Australia); Bass Strait (Tasmania); Port Phillip Heads and Westernport Bay (Victoria); Torres Straits, Cape York, and GBR (Queensland); also recorded from the SW Pacific (New Caledonia), NW Pacific (Japan), Indian Ocean (Seychelles, Ceylon (Sri Lanka), and amphi-Atlantic (Florida, Bermudas, Brazil, Portugal).

DESCRIPTION. *Growth form.* The cormus is composed of large anastomosing, round to flattened tubes up to 1cm diameter. The round tubes (<5mm diameter) partly stand vertically about 1cm above the rest of the cormus and possess a terminal naked osculum, about half the size of the tube. The main part of the cormus is flat, with only few naked oscules scattered on ridges of the anastomosing tubes.

*Colour.* White in life, beige after fixation with Glutaraldehyde in EtOH.

*Oscules.* A few naked oscules are scattered on the ridges of anastomosing tubes, or are terminal at the top of vertical tubes. The diameter of ridge oscules are smaller (<1.5mm) than terminal oscules (<3mm).

*Texture.* Harsh, relatively firm, slightly rough.

*Surface ornamentation.* Surface is unornamented, although it appears coarse due to the presence of large tangential triactines in the cortex.

*Ectosomal skeleton.* A distinct cortex is developed, 100-170µm thick, consisting of a tangential layer of regular, cylindrical, more-or-less sharply pointed large triactines. The angle between two rays is occasionally greatly enlarged (up to nearly 180°), in which case these triactines become sagittal, or one actine may be sharply bent at its top, or the actines may be slightly undulated. Up to five triactines are densely stacked above each other without any apparent alignment, but in a way that space is maintained the actines for vertical sub-circular inhalant canals. Occasional, large, regular tetractines are regularly dispersed directly beneath the distinct cortex. The basal triradiate systems of these enormous tetractines are tangentially arranged in the subcortical layer, between cortex and choanosome, with their apical actines penetrating the choanosome and protruding through the atrial surface into the atrium.

*Choansomal skeleton.* The choanosomal skeleton is only supported by small scattered cylindrical regular triactines and tetractines, with a regular basal triradiate system, 300-500µm thick. One actine of the regular triactines often points in the direction of the atrium, but actines are also sometimes irregularly aligned. Apical actines of tetractine spicules often point towards the atrium, but these are also often tangentially aligned around the radially arranged, branching and elongated choanocyte chambers. In this latter case their free apical actines protrude into the choanocyte chambers. Furthermore, a distinct atrial skeleton is supported by small sagittal triactines and tetractines which are embedded in a thin atrial membrane. Their unpaired actines or apical actines, respectively, protrude through the atrial membrane into the atrium. The free apical actine of atrial tetractines is often slightly undulated, and in rare cases it may be slightly enlarged.

*Aquiferous system.* Numerous inhalant canals, up to 150µm diameter, are located between tangential cortical triactines, suppling choanocyte chambers with water. These inhalant canals are covered by a thin membrane, pierced by several ostiae above each canal. Ostiae have a diameter of 40-60µm. Choanocyte chambers, elongated and branch irregularly, 80-160µm diameter, are radially arranged around the atrium. These open through the atrial membrane into the atrium. The aquiferous system has a syconoid grade of construction, and although choanocyte chambers are irregularly branched, they maintain a general radial organisation.

*Soft tissue.* Thin ectosomal exopinacoderm covers the tangentially arranged triactines of the cortex and incurrent canals. Above the incurrent canals, the exopinacoderm is pierced by several ostiae (see above for dimensions). Cortical triactines are embedded in a relatively thin mesohyle with only a few visible cells, probably archaeocytes and/or sclerocytes. The choanosome consists of elongated, irregularly branching choanocyte chambers, where choanocytes densely line all walls of chambers. Choanocytes are 4-6µm in diameter, and are sub-spherical, tetragonal to hexagonal in shape in section parallel to the surface. Only few archaeocytes were observed in the choanosome. Choanocyte chambers open via 50-150µm wide openings through the thin atrial membrane (10-15µm thick), into the central atrium. The atrial membrane contains only few cell-types, of which some are amoeboid and may be archaeocytes, and others are more spherical and resemble choanocytes (although no flagella were seen and

it is not possible to determine if they are choanocytes without higher resolution microscopy (in progress).

*Spicules.* Regular cortical triactines, sometimes sagittal (t-shaped, with unpaired angle up to 180°), 105-(285.2)-470×15-(38.28)-60µm (n=25); Large regular subcortical tetractines, 320-(532.5)-630× 70-(100)-130µm (n=4); Regular choanosomal triactines with cylindrical actines and blunt (rounded) tips, 54-(63.76)-70×2-(2.48)-4µm (n=25); Regular choanosomal tetractines with cylindrical actines, same size and shape of the basal triradiate system as the choanosomal triactines, but with a reduced apical actine; Sagittal atrial triactines with cylindrical actines and blunt (rounded tips), longer paired actines 48-(51.88)-62×2-(4)-7µm (n=25), shorter unpaired actine 32-(40.44)-56 (n=25), the shorter unpaired actine is often slightly thinner than the longer paired actines; Sagittal atrial tetractines, same size and shape of the basal triradiate system as the choanosomal triactines, but with a reduced apical actine.

REMARKS. *Leucaltis clathria* was initially described by Haeckel (1872) from Florida, and subsequently recorded in many parts of the world (see above). It was recorded from the N coast of Qld. (Cape York, Torres Strait) by Poléjaeff (1883) as '*Heteropegma nodus gordii*', which is allegedly synonymous with *L. clathria*. The specimen described here from Heron Island is the first record of this species from the GBR. It is morphologically indistinguishable from *L. clathria*, as described by Haeckel (1872), and *H. nodus gordii*, as described by Poléjaeff (1883), in having very similar skeletal structure, spicule sizes, shapes and varieties, as well as irregular radial choanocyte chambers. *Leucaltis clathria* is allegedly cosmopolitan, with all recorded specimens having these very characteristic and unique morphological and organisational features, despite populations being widely dispersed and discontiguous. Although the taxonomic status of allopatric populations of so-called 'cosmopolitan species' is still not clearly resolved for most sponge groups (e.g. Solé-Cava et al., 1991, Klautau et al., 1994, Wörheide, 1998), we are presently unable to find any morphological characters to differentiate GBR populations of *L. clathria* from other populations in other parts of the world (Haeckel, 1872; Poléjaeff, 1883; Dendy, 1913; Borojevic & Klautau, in press). More sophisticated biological tools (e.g. PCR profiles), are required to resolve this problem, currently beyond the scope of the present project.

## Family **Leucettidae** de Laubenfels, 1936

Clathrinida with a solid body. The aquiferous system is always leuconoid. The choanoskeleton is well-developed and in the form of a regular network composed of triactines and/or tetractines. The cortex is thin and composed of spicules similar to those of the choanoskeleton (*sensu* Borojevic, 1968).

### **Leucetta** Haeckel, 1872

*Leucetta* Haeckel, 1872: 116.
*Leucettaga* Haeckel, 1872: 117.
*Teichonella* Carter, 1878: 35.

Leucettidae with a homogeneous organisation of the wall and a typical leuconoid aquiferous system. There is neither a clear distinction between the cortex and the choanoskeleton, nor the presence of a distinct layer of subcortical inhalant cavities. The atrium is frequently reduced to a system of exhalant canals that open directly into the osculum.

### **Leucetta microraphis** Haeckel, 1872 (Fig. 8A-G, Table 2)

*Leucetta microraphis* Haeckel, 1872: 119, pl. 21, figs 10-17; Dendy & Row, 1913: 734; Dendy & Frederick, 1924: 482; Row & Hozawa, 1931: 746; Tanita, 1942: 111, pl. 6, fig. 4; Borojevic, 1967: 3, fig. 2; Borojevic & Peixinho, 1976: 1003, fig. 9; Pulitzer-Finali, 1982: 48, Fig. 1; Borojevic & Klautau, in press.
*Leucetta primigenia microraphis* Haeckel, 1872:119, pl. 21, figs 10-17; Ridley, 1884: 482.
*Leuconia dura* Poléjaeff, 1883: 65, pl. 2, fig.3, pl.7, fig.7.
*Pericharax carteri homoraphis* Poléjaeff, 1883: 66.
*Leucaltis floridana australiensis* Carter, 1886: 145.
*Leucandra carteri* Dendy, 1893: 103.
(see Burton, 1963: 270, and Borojevic, 1967: 3, for detailed synonymy)

MATERIAL. HOLOTYPE: No clear segregation of surviving syntypes into respective type localities. SYNTYPES: PMJ Porif.106, '*Leucetta microraphis* (*L. primigenia* var.)/Mare Rubrum/Frauenfeld' (NMV photos 56/26–29). Type locality: Red Sea, possibly also Gulf of St. Vincent, South Australia. OTHER MATERIAL: QMG313659, Wistari Reef, Wistari Channel, GBR, 23°27.5'S, 151°55'E, 17m depth, 06.vii.1998, coll. G. Wörheide (SCUBA).

HABITAT AND DISTRIBUTION. Steep wall, small crevices under coral, Zone 1 (Fig. 2); also known to live in exposed and semi-shaded areas of coral reefs. Allegedly cosmopolitan. Recorded distribution in Australia: Qld (Torres Strait; Heron I., Wistari Reef, S GBR), SE coast (Bass Strait), New South Wales (Port Jackson to Shark Is), Victoria (Port Phillip Bay), Western Australia (Houtman

TABLE 2. Statistical comparison of the most abundant type of small triactines between *Leucetta microraphis*, *Leucetta chagosensis* and *Leucetta villosa* sp. nov. Measurements in µm (n=30).

| Species | *L. microraphis* | | *L. chagosensis* | | | | | | *L. villosa* | |
|---|---|---|---|---|---|---|---|---|---|---|
| Sample | QMG313659 | | QMG313654 | | QMG313658 | | QMG313667 | | QMG313662 | |
| | Length | Width | Length | Width | Length | Width | Length | Width | Length | Width |
| Mean | 169.4 | 18.2 | 126.4 | 18.1 | 134.1 | 15.4 | 128 | 16.4 | 118.3 | 16.3 |
| Std Dev. | 19.4 | 2.6 | 11.9 | 1.7 | 11.4 | 1.7 | 9.1 | 1.6 | 8.3 | 2.1 |
| Min. | 140 | 14 | 98 | 14 | 118 | 12 | 112 | 14 | 100 | 12 |
| Max. | 240 | 28 | 144 | 22 | 158 | 18 | 148 | 20 | 134 | 20 |

Abrolhos, Shark Bay, Geraldton, Bunbury); also reported from the Mediterranean, amphi-Atlantic, S Atlantic, amphi-Pacific, Indian Ocean, S Africa, Red Sea and Antarctica.

DESCRIPTION. *Growth form*. With a massive, convoluted, lamellate growth form, 3×4cm in size, and one 'finger-like' protrusion, 1.5cm long, 0.5cm wide.

*Colour*. Brownish-yellow to greenish-yellow in life, beige after fixation in Glutaraldehyde in EtOH.

*Oscules*. A few small naked oscules without 'lip' are scattered on ridges of the sponge and terminal on the finger-like protrusion, 1-2mm diameter.

*Texture*. Firm, harsh.

*Surface ornamentation*. Smooth.

*Ectosomal skeleton*. A distinct dense cortex of tangential small regular triactines is developed, with a thickness of 60-100µm. A few tangentially orientated large ('giant') triactines are also present in the cortex. The cortex is followed inwards by a prominent layer of subdermal cavities (40-200µm diameter). This zone of subdermal cavities, up to 250µm thick, is the transition zone between surface and choanoome. The zone of subdermal cavities is composed of irregularly arranged, but mostly perpendicular aligned small triactines, with a few scattered large 'giant' triactines between. A peculiar form of small sagittal triactine and tetractine is only found in the small oscular rim. In this spicule type all three actines have the same total length, and the angles between the actines are equal, but both paired actines of the triactine (or of the basal triradiate system of the tetractine, respectively), are bent from each of their actinal center about 30° towards the unpaired actine (Fig. 8C-F). Sagittal triactines and tetractines have the same dimensions in their triradiate system, and the apical actine of the sagittal tetractine is either straight, or slightly bent at the distal end.

*Choanosomal skeleton*. Regular triactines of two very different sizes form an irregular meshwork in the choanosome, with a relatively low density, leaving space for the choanocyte chambers. Large 'giant' triactines are present, occasionally scattered throughout the choanosome between the numerous smaller triactines. No pattern of alignment was recognised between both size classes of triactines in the choanosome, although small triactines are found tangentially aligned and densely packed around incurrent canals, where they form the walls of these canals. Similarily, sagittal tetractines are found only around exhalant canals, with their basal triradiate system tangentially arranged, forming the walls. Their free apical actines protrude into the excurrent canal.

*Aquiferous system*. Water enters the sponge through ostiae (although none were observed in sections studied), via subdermal cavities located below the cortex. These cavities open into larger incurrent canals which lead into the choanosome. The water leaves the choanosome initially through small excurrent canals, which open into larger canals leading to the osculae. These larger canals are often flattened, measuring about 0.5x1mm. Both incurrent and excurrent canals maintain a general radial orientation. The aquiferous system has a leuconoid grade of construction.

*Soft tissue*. The soft tissue of the cortex has an extremely dense appearance. It is free of choanocytes, but contains numerous amoeboid archaeocytes (up to 14µm diameter). The early stages of spherical oocytes (8-10µm diameter), are far more abundant, mostly opaque, sometimes granular, and rarely translucent. They posses a distinct central area (90% of their diameter), and always have a translucent thin rim (possibly a cell coat). Sometimes two-cell embryos were observed. Oocytes are predominant in, but not restricted to, the cortex, scattered in varing numbers in other parts of the soft tissue. The choanosome is dense, with sub-spherical to

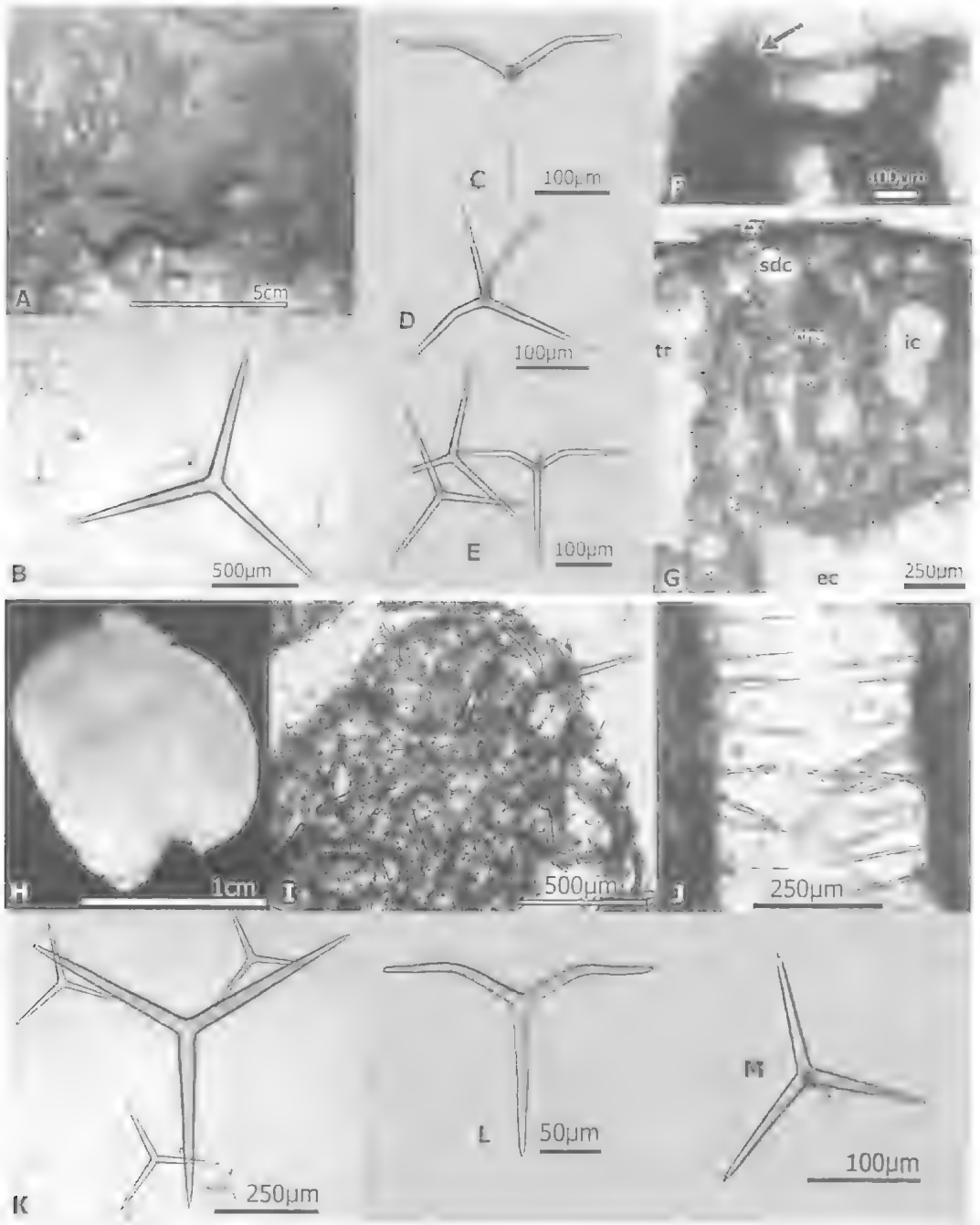



FIG. 8. *Leucetta* spp. A-G, *Leucetta microraphis* Haeckel, 1872 (specimen QMG313659). A, a specimen in situ. B, two sizes of triactines. C, oscular sagittal tetractine. D, oscular sagittal tetractine. E, oscular sagittal tetractine (left) and two regular tetractines. F, cross-section of an osculum with one oscular triactine (arrow). G, cross-section of cortex (cx) and choanosome (chs) with sub-dermal cavities (sdc), a large 'giant' triactine (tr), incurrent (ic) and excurrent (ec) canals. The little black dots are oocytes. H-M, *Leucetta chagosensis* Dendy, 1913 (specimen QMG313654). H, specimen after fixation. I, cross-section of choanosome. J, section of an excurrent canal with free apical actines of tetractines pointing into canal. K, three size classes of triactines (smallest one is young) and one tetractine (bottom center). L, sagittal triactine of the oscular rim ('lip'). M, tetractine of the excurrent canal with reduced apical actine.

spherical choanocyte chambers, 50-60µm diameter. Choanocytes are sub-spherical to spherical, 2-4µm diameter.

*Spicules*. Large 'giant' regular triactines with conical actines, 460-(705.2)-940×60-(120)-91.2µm (n=25); small triactines with conical actines 140-(169.4)-240×14-(18.2)-28µm (n=25); sagittal tetractines of exhalant canals, with more cylindrical actines, and their free actine curved 110-(143.4)-165×12-(14.4)-20µm (n=25); small sagittal triactines and tetractines of the oscular rim (both the same size) 70-(122.9)-160×10-(12.4)-16µm (n=14). In this latter spicule type all three actines have the same total length, where the unpaired angle is slightly enlarged and both paired actines of the triactine (or of the basal triradiate system of the tetractine, respectively), are bent below their actinal center, about 30° towards the unpaired actine (Fig. 8C-F). Sagittal triactines and tetractines have the same dimensions in their triradiate system, and the apical actine of sagittal tetractines is either straight, or slightly bent at the distal end.

REMARKS. The allegedly cosmopolitan distribution of *L. microraphis* is disputed here, but there is currently no additional empirical support to resolve this problem one way or another, based on 'classical' morphological criteria

**Leucetta chagosensis** Dendy, 1913
(Fig. 8H-M, Table 2)

*Leucetta chagosensis* Dendy, 1913: 10, pl. 1, fig. 6, pl. 4, fig. 2; Dendy & Row, 1913: 733; Dendy & Frederick, 1924: 482; Burton, 1963: 241; Borojevic, 1967: 2, fig. 1; Pulitzer-Finali, 1982: 89; Borojevic & Klautau, in press.

*Leucetta infrequens* Row & Hozawa, 1931: 747, pl. 19, fig. 4.

*Leucetta expansa* Row & Hozawa, 1931: 749, pl. 19, fig. 5.

MATERIAL, HOLOTYPE: BMNH1920.12.9.51, 'Sealark Collection' (CXIX 11), Salomon (Chagos Archipelago). OTHER MATERIAL: QMG313654, Tenements, Heron I., GBR, 23°26.05'S 151°57.1'E, 15m depth, 22.vi.1998, coll. G. Wörheide (SCUBA); QMG313658: Wistari Reef, Wistari Channel, GBR, 23°27.5'S, 151°55'E, 17m depth, 06.vii.1998, coll. G. Wörheide (SCUBA); QMG313667, S side of Wistari Reef, GBR, 23°29.4'S, 151°52.8'E, 18m depth, 07.vii.1998, coll. G. Wörheide (SCUBA).

HABITAT AND DISTRIBUTION. In crevices and under overhangs of coral bommies, also abundant in illuminated reef habitats, Zones 1-2 (Fig. 2). Indo-west Pacific: Recorded distribution in Australia: Western Australia (Houtman Abrolhos, Fremantle), Queensland (Heron I., S GBR); also Indian Ocean (Chagos) and W Pacific (New Caledonia).

DESCRIPTION. *Growth form*. Massive, globular, slightly elongated-globular to pyriform, elongate. Specimens range from 1-5cm.

*Colour*: A distinct bright yellow colour in life, brownish-beige after fixation with Glutaraldehyde in EtOH.

*Oscules*. Globular to pyriform specimens have one prominent oscule with a naked 'lip' at the apical end of the body. Elongated specimens have a few oscules with a naked 'lip' scattered on the ridge of the sponge body.

*Texture*. Firm and smooth, not harsh, soft compared to *L. microraphis*, slightly translucent surface.

*Surface ornamentation*. Surface is unornamented, although sometimes small protuberances are present on elongated specimens.

*Ectosomal skeleton*. A distinct thin cortex, up to 50µm thick, is supported by tangentially arranged small regular triactines, with some large triactines also scattered tangentially in the cortex. Small sub-dermal cavities (50-150µm diameter) are present, with their walls partially formed by bundled actines of perpendicular triactines of the upper choanosome. The zone of sub-dermal cavities, which is devoid of choanocyte chambers, is up to 250µm thick. Large regular triactines are also found in the zone of sub-dermal cavities, either tangentially aligned, or scattered perpendicular to the surface. A peculiar, special, small sagittal triactine is only found in the oscular rim ('lip'), where both paired actines are bent from each of their actinal center about 30° towards the unpaired actine (Fig. 8L).

*Choanosomal skeleton*. A dense meshwork of numerous small regular triactines, aligned in such a way that they form an irregular, sometimes sub-hexagonal to hexagonal pattern with their actines. Choanocyte chambers are located within the free space provided within this hexagonal or irregular network. Larger triactines are occasionally scattered and irregularly arranged in the choanosome in variable numbers (usually only a few are present), but never reaching the high numbers of small triactines. Small tetractines are found concentrated in the exhalant canals, with their basal triradiate system tangentially aligned to form the walls of canals, and their mostly straight and elongated free apical actine protrudes into the canal. Tetractines were only very rarely found in the choanosome, and when present, they were in close proximity to a canal. The number of tetractines varies from

specimen to specimen.

*Aquiferous system*. Water enters the sponge body via ostiae (20-50µm diameter) and incurrent canals, which pierce the cortex in spaces between tangential triactines. These incurrent canals are 50-100µm wide and become wider below the sub-dermal cavities to supply the choanosome with sea water. Walls of the incurrent canals in the choanosome are only rarely formed by tangentially aligned triactines, whereas mostly canals are found between the hexagonal network formed by triactines aligned perpendicular to canals. Walls of exhalant canals, in contrast, are formed by the tangentially aligned basal triradiate system of tetractines. These canals are wider than incurrent canals and open in an irregular pattern into the more-or-less wide atrium, which never reaches the dimensions of those seen in *Pericharax heteroraphis*. The aquiferous system has a leuconoid grade of construction.

*Soft tissue*. Soft tissue of the cortex is free of choanocytes but contains some scattered amoeboid cells, probably archaeocytes, up to 10-30µm long. The choanosome follows the cortex without a sharp transition. Choanocytes are sub-spherical, 4-8µm diameter in section parallel to the surface, and choanocyte chambers are spherical, 80-100µm diameter. Water canals are lined by the endopinacoderm, which consists of relatively large and stretched pinacocytes (up to 12µm long).

*Spicules*. Larger regular triactines with conical actines, actines: 250-(361)-500x25-(34.7)-50µm (n=25); smaller regular triactines with conical actines, actines: 98-(129.5)-158x 12-(16.7)-22µm (n=30); regular tetractines of the excurrent canals with cylindrical actines 93-(107.3)-125× 10-(12.8)-18µm (n=25); rare sagittal triactines of oscular rim ('lip') 70-(88.6)-120×9-(11.4)-15µm (n=7). In this latter spicule type all three actines have the same total length, the unpaired angle is slightly enlarged than or equal to the paired angles, and both paired actines of the triactine are each bent from or below their actinal center about 30° towards the unpaired actine (Fig. 8L).

**Leucetta villosa** sp. nov.
(Fig. 9A-F, Table 2)

ETYMOLOGY. For the hair-like extensions on the sponge surface (Latin, *villosus*).

MATERIAL. HOLOTYPE: QMG313662, S side of Wistari Reef, GBR, 23°29.4'S, 151°52.8'E, 18m depth, 07.vii.1998, coll. G. Wörheide (SCUBA).

HABITAT AND DISTRIBUTION. Coral patches, small crevices and overhangs under coral bommies, Zone 2 (Fig. 2), 18m depth. Wistari Reef, S GBR.

DESCRIPTION. *Growth form*. Massive, convoluted-lobate, 5×5×3cm.

*Colour*. Yellow-brownish in life, bright beige after fixation in Glutaraldehyde in EtOH.

*Oscules*. Many oscules, 2-5mm diameter, on ridges of the sponge body. Oscules possess a small naked 'lip'.

*Texture*. Firm but not harsh, slightly translucent surface.

*Surface ornamentation*. The surface has characteristic 'hairy' surface extensions, which protrude 1-3mm above the external surface.

*Ectosomal skeleton*. A distinct, thin cortex, up to 50µm thick, is supported by tangentially arranged small regular triactines, with some large triactines also scattered tangentially in the cortex. Small sub-dermal cavities (50-100µm diameter) are only infrequently developed, and where present, their walls are partially formed by the bundled actines of perpendicular triactines from the upper choanosome. A sub-cortical zone, which is devoid of choanocyte chambers, is present in some parts of the sponge, approximately 100-150µm thick. Where the subcortical zone is absent, the choanosome follows sharply under the cortex. Large regular triactines are also found in places within the sub-dermal zone, and where present, they are either tangentially aligned, or scattered perpendicular to the surface (then protruding into the choanosome). Unlike *L. chagosensis*, there are no peculiar small sagittal triactines in the oscular rim.

*Choanosomal skeleton*. A dense meshwork of numerous small regular triactines, aligned in such a way that they form an irregular, sometimes sub-hexagonal to hexagonal pattern with their actines. Choanocyte chambers are located in the free space provided within this meshwork, sometimes hexagonal but mostly forming irregular patterns. Larger triactines are scattered and irregularly arranged within the choanosome in moderate numbers, but never reaching the high abundance of small triactines. Small tetractines are not very common and mostly found concentrated in the larger exhalant canals, with their basal triradiate system tangentially aligned to form the walls of canals. Their mostly straight, free apical actine protrudes into the canal. Rare tetractines were also found in the choanosome.

*Aquiferous system*. Water enters the sponge body via ostiae (although not seen in sections) and

incurrent canals, which pierce the cortex in the space between tangential triactines. These incurrent canals are 50-100µm wide and become wider below the sub-dermal cavities to supply the choanosome with sea water. Walls of the incurrent canals in the choanosome are only rarely formed by tangentially aligned triactines, whereas mostly canals are found between the sub-hexagonal to spherical network produced by triactines aligned perpendicular to the canal. Walls of the exhalant canals, in contrast, are formed by tangential triactines and the tangentially aligned basal triradiate system of tetractines. These canals are wider than incurrent canals and open, in an irregular pattern, into larger excurrent canals (up to 5mm diameter), which may fuse just below the osculum. No single central large atrium is present. The aquiferous system has a leuconoid grade of construction.

*Soft tissue*. Soft tissue of the cortex is free of choanocytes and only rarely contains amoeboid cells, most likely archaeocytes, up to 6-10µm long. The choanosome follows the cortex without a sharp transition. Choanocytes are sub-spherical, 3-6µm diameter in section parallel to the surface, choanocyte chambers are spherical, 70-100µm diameter.

*Spicules*. Larger regular triactines with conical actines, sometimes slightly parasagittal (unpaired actine slightly longer): 300-(405.5)-490x30-(37.4)-40µm (n=25); smaller regular triactines with conical actines: 100-(118.3)-134x12-(16.3)-20µm (n=30); few regular conical tetractines with reduced undulated apical actine 95-(105)-120x10-(13.1)-16µm (n=25).

REMARKS. *Leucetta microraphis* and *L. chagosensis* have been previously reported from the GBR (Heron Island and Wistari Reef) by Pulitzer-Finali (1982), and from Torres Strait by Ridley (1884) and Poléjaeff (1883, as *Leuconia dura*), but none of this material was comprehensively or adequately described. Furthermore, it appears that Pulitzer-Finali (1982) misidentified his specimens of '*L. microraphis*'. The specimen depicted in his Figure 1 is more probably *Pericharax heteroraphis*, due to its possession of an irregularly folded external surface and a wide central osculum, both highly characteristic for *P. heteroraphis* (see below). *Leucetta microraphis* is clearly different in having: 1) multiple small oscules (nowhere near the size in the specimen figured by Pulitzer-Finali (1982)); 2) no folded external surface; and 3) no 'ample internal cavity' (Pulitzer-Finali, 1982), but shares the large ('giant') triactines. The peculiar small sagittal triactines and tetractines described here from the oscular rim of the GBR *Leucetta microraphis*, were also described by Borojevic & Peixinho (1976) from their specimen from Brazil, but due to the presence of large 'giant' tetractines in the cortex of the Brazilian specimen, Borojevic & Klautau (in press) suggested it might be more appropriately placed in the Atlantic '*Leucetta floridana*' (Haeckel, 1872) complex (with 'giant' tetractines), which is supposedly a sibling species of *L. microraphis*.

Differentiating between species of *Leucetta* is similar to the problems described above for *Clathrina*, largely due to the possession of only few diagnostically important morphological characters (i.e. two types of triactines). Consequently, statistical analysis of the most frequent category of spicule (small triactines) was undertaken for three specimen *of L. chagosensis*, and one each of *L. microraphis* and *L. villosa* (Table 2). Pairwise comparisons between actinal length of 30 spicules for each specimen, using a Student t-test, showed that the means of G313659 (*L. microraphis*) and G313662 (*L. villosa*) were significantly different at a confidence level of 99% ($t=2.663$, with $P<0.01$) compared to each other, and compared to the means of *L. chagosensis* (G313654, G313658 and G313667). The means of the latter three specimens were not significantly different compared to each other ($t=2.663$, $P>0.01$). These three specimens agree with the description of *L. chagosensis*, based on their morphological features and characteristic bright-yellow color, as described by Dendy (1913) and Borojevic (1967). The peculiar sagittal triactines in the oscular rim of *L. chagosensis*, as described by Borojevic (1967: Fig. 1D) from New Caledonia, were also found in *L. chagosensis* from the GBR. In addition to having significantly different mean dimensions in actinal spicule lengths, *L. microraphis* is clearly characterised by the presence of large ('giant') triactines (not present in other species of *Leucetta*), its distinct growth form, color, texture, and the relatively small size of its choanocyte chambers (50-60µm diameter). The peculiar sagittal triactines and tetractines found around the small oscular rim of *L. microraphis* were also mentioned by Poléjaeff (1983: 65, Pl. 7, Fig 7) in his description of *'Leuconia dura'*, which is a junior synonym of *L. microraphis* (Burton, 1963; Borojevic, 1967). Compared to *L. chagosensis* and *L. microraphis*, *L. villosa* can be

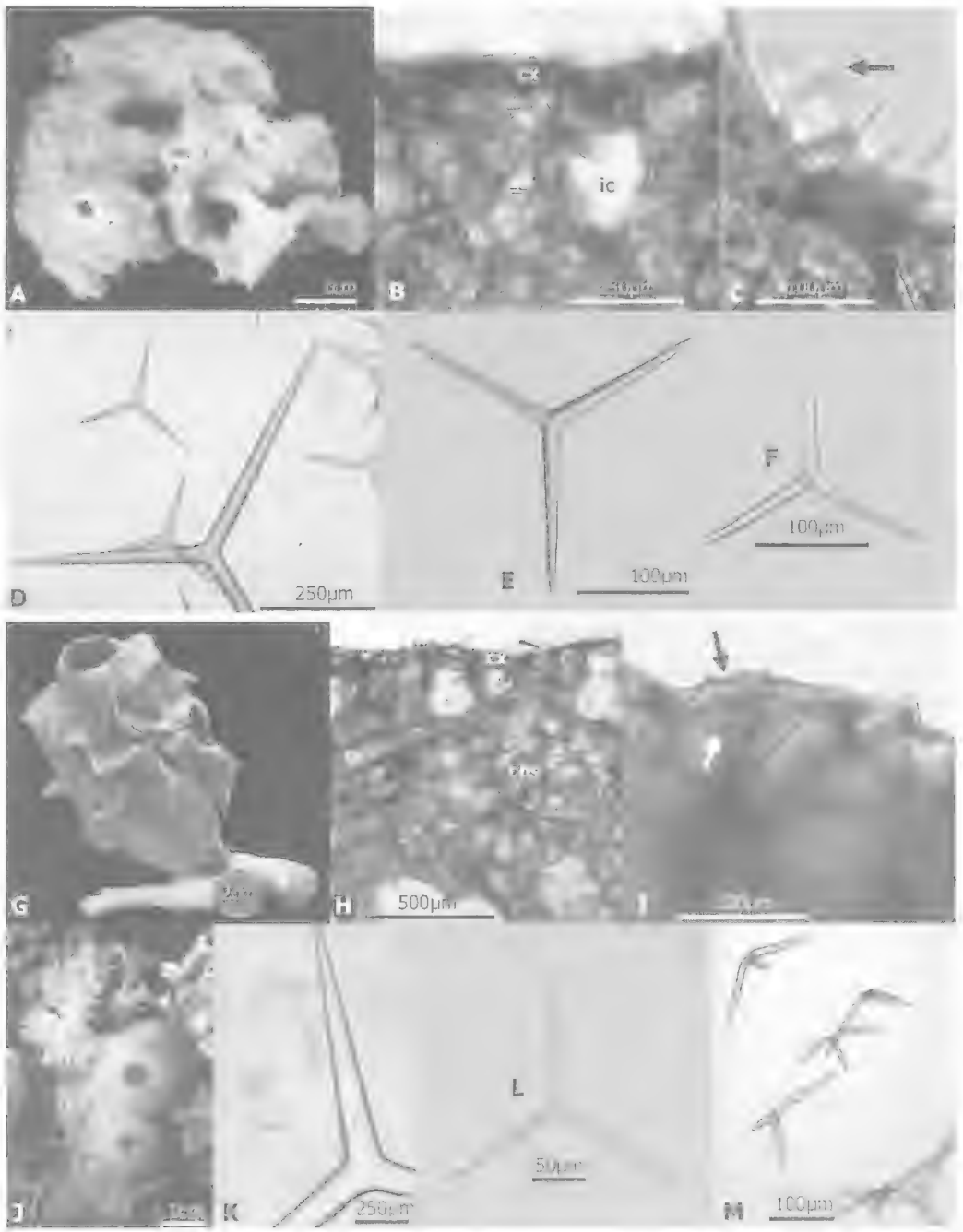



FIG. 9. *Leucetta* and *Pericharax* spp. A-F, *Leucetta villosa* sp. nov. (holotype QMG313662). A, specimen after fixation. B, section through the cortex (cx), choanosome with irregularly arranged triactines and one incurrent canal. C, excurrent canal with free apical actines of tetractines pointing into canal (arrow). D, two size classes of triactines. E, small triactine with conical actines. F, tetractine. G-M, *Pericharax heteroraphis* Poléjaeff, 1883 (specimen QMG313653, in situ photograph, sections, spicules). G, dried larger specimen with irregularly folded external surface and one large central osculum. H, section through cortex (cx) and choanosome (chs) with large triactines (tr). I, enlargement of the cortex with 'tripod-like' triactines (arrows), characteristic for *P. heteroraphis*. J, two small specimen in situ at Wistari Reef (center), together with *Soleniscus radovani* sp. nov. (upper left). K, two size classes of triactines. L, tetractine. M, 'tripod-like' triactines (compare with Fig. 9I).

distinguished by statistically significant differences in the mean actinal lengths of small triactines (at a confidence level of 99%; Students *t*-test, pairwise comparisons, t=2.663, P<0.01), its distinct growth form, color, hirsute surface, the absence of small sagittal triactines in the oscular rim, and the different mean lengths of its large triactines.

Tropical and subtropical species of *Leucetta*, together with *Pericharax heteroraphis*, are the most common and abundant calcareous sponges in the exposed and semi-cryptic habitats of the GBR. Regional populations of these species certainly require a comprehensive morphological and genetic study, and thorough taxonomic revision. These studies, (population genetics, intraspecific morphological variation, molecular and morphological analyses) are currently in progress and will hopefully provide valuable new information on the taxonomy of this important species complex of *Leucetta*, particularly of GBR species.

### **Pericharax** Poléjaeff, 1883

*Pericharax* Poléjaeff, 1883: 66.

Leucettidae with a large central atrium surrounded by a thick wall. The wall is divided into a choanoderm and a thin subcortical layer of inhalant cavities, supported by a peculiar skeleton partially composed of the centripetal actines of the special cortical triactines.

### **Pericharax heteroraphis** Poléjaeff, 1883 (Fig. 9G-M)

*Pericharax carteri heteroraphis* Poléjaeff, 1883: 66, pl. 2, fig. 5, pl. 7, fig. 8.

*Pericharax heteroraphis*; Dendy, 1913: 13; Dendy & Row, 1913: 735; Burton, 1963: 260, text-fig. 126; Wilkinson, 1978a: 162; Wilkinson; 1978b: 172; Wilkinson, 1978c: 178, fig. 1; Wilkinson 1979: 794.

*Pericharax peziza* Dendy, 1913: 15, pl. 1, fig. 9, pl. 5, figs 3-4; Dendy & Row, 1913: 735; Burton, 1930: 3; Burton, 1934: 518.

*Pericharax pyriformis* Burton, 1932: 258, pl. 48, figs 1-2.

MATERIAL. HOLOTYPE: BMNH1884.4.22.56-57, Tristan Da Cunha, 'Challenger' Collection. OTHER MATERIAL: QMG313652, QMG313653, Tenements, N side of Heron I., GBR, 23°26.05'S 151°57.1'E, 15m depth, 22.vi.1998, coll. G. Wörheide (SCUBA); QMG313657, Wistari Reef, Wistari Channel, GBR, 23°27.5'S, 151°55'E, 17m depth, 06.vii.1998, coll. G. Wörheide (SCUBA); QMG313660, S side of Wistari Reef, GBR, 23°29.4'S, 151°52.8'E, 18m depth, 07.vii.1998, coll. G. Wörheide (SCUBA).

HABITAT AND DISTRIBUTION. Widely distributed in exposed and semi-shaded habitats of coral reefs, sometimes under overhangs, Zones 1-2 (Fig. 2). Widely distributed, allegedly nearly cosmopolitan. Reported distribution in Australia: GBR (Qld), Pascoe Reef, Papuan Pass; also S Atlantic, Indian Ocean, Indo-Malayan region and Subantarctic.

DESCRIPTION. *Growth form*. Massive, bulbous, rarely clavate. Young (small) specimens pyriform, with external surface not folded; large (older) specimens with characteristic irregularly folded external surface. Maximum size observed for the species was 25cm in height (specimen from Lizard Island, N GBR).

*Colour*. Yellow-greenish to dark greenish-brown in life and brownish after fixation with Glutaraldehyde in EtOH

*Oscules*. One large prominent terminal osculum always present, mostly with prominent 'lip'.

*Texture*. Firm, harsh, surface smooth but brittle due to large triactines protruding through the surface.

*Surface ornamentation*. Smooth in small specimens, irregularly folded in large specimens.

*Ectosomal skeleton*. A thin but distinct cortex is present, up to 50µm thick, consisting of tangentially aligned, small, characteristic tripod–like triactines, sometimes sagittal, with curved paired actines. Both small and large triactines are also present, with the former tangential or perpendicular to the surface, and the latter more-or-less tangentially arranged. Subdermal cavities are present in most areas below the cortex (50-200µm diameter), and are supported in their lower regions by perpendicularly 'bundled' actines of small choanosomal triactines, forming a distinct sub-cortical skeleton, devoid of choanocyte chambers. The zone of sub-dermal cavities is up to 400µm thick. Scattered large triactines are also arranged parallel to the surface in the sub-dermal area.

*Choanosomal skeleton*. A dense meshwork of mainly regular small triactines forms the choanosomal skeleton. These small triactines are aligned in such a way that their actines form an irregular, often sub-hexagonal to hexagonal pattern. choanocyte chambers are located between the sub-hexagonal to hexagonal, or sometimes irregular skeletal meshwork. Some small tetractines are also found scattered throughout the choanosome, without any apparent order or alignment. Many large 'giant' triactines are dispersed throughout the choanosome without any recognisable order. Small tetractines are concentrated at, but not restricted to, the excurrent water canals. Their tangential basal triradiate system

forms the wall of canals, and the shorter and curved free apical actine protrudes into the exhalant water canal and atrium.

*Aquiferous system*. Water enters the sponge body via ostiae (30-50µm diameter) and incurrent canals, which pierce the cortex in the space between tangential triactines. These incurrent canals, 100-200µm wide, become wider below sub-dermal cavities in order to supply the choanosome with sea water. Walls of the incurrent canals in the choanosome are only rarely formed by tangentially aligned triactines, whereas canals are mostly found between the hexagonal network formed by triactines aligned perpendicular to the canal. Walls of the exhalant canals are more frequently formed by tangentially aligned basal triradiate system of tetractines and by tangential triactines. These excurrent canals are much wider than incurrent canals and open in a regular pattern into the wide central atrium The surface of this central atrium resembles, in larger specimens, a 'sieve'-like surface with regularly sized (0.5mm), and densely arranged openings. The aquiferous system has a leuconoid grade of construction.

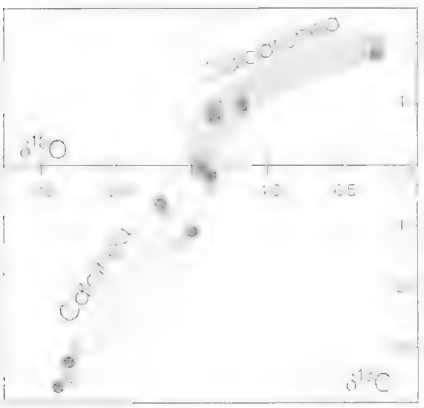
*Soft tissue*. The cortex and the zone of sub-dermal cavities is devoid of choanocyte chambers, but many other cell-types are present. Most of these are spherical or amoeboid, some contain small granules, ranging in size 4-18µm. It is not yet certain but it is likely that the amoeboid cells are archaeocytes, the granular cells are some type of storage cell, and the spherical cells possibly oocytes. Some cells are 'wrapped' and attached to spicules, and are probably sclerocytes. The choanosome follows the cortex with a more-or-less sharp transition and is dense. Spherical choanocyte chambers are 80-120µm diameter, with sub-spherical to polygonal choanocytes (4-6µm diameter in section parallel to the surface). A few apopyles were observed, up to 35µm diameter, lined by two to three elongated apopylar cells.

*Spicules*. Large regular triactines with conical actines, with actines: 550-(834)-1570×70-(108.6)-180µm (n=25); smaller regular triactines with more-or-less cylindrical actines, with actines: 120-(159.4)-190×15-(18.64)-22µm (n=25); tetractines with a mostly regular basal triradiate system and slightly shorter and curved apical actine, sometimes one or two actines of the basal triradiate system are bent, sometimes the basal triradiate system is slightly parasagittal, with the actines of the regular basal triradiate system: 90-(128.4)-180×10-(12.16)-18µm (n=25); tripod-like cortical sagittal triactines, with curved paired actines: 45-(93.8)-130× 7-(10)-15µm (n=25), with the unpaired actine sometimes slightly either shorter or longer, and the unpaired angle is larger than the paired angles.

REMARKS. *Pericharax heteroraphis* is the most common calcareous sponge in exposed and semi-cryptic habitats throughout the GBR and other tropical seas of the Indo-Pacific. Large specimens of *P. heteroraphis* are easily differentiated macroscopically from the highly abundant *Leucetta* spp. by their distinct greenish-brown color and their irregularly folded external surface. However, small specimens do not show a distinct surface folding and sometimes closely resemble *Leucetta chagosensis* in growth form, although most can be distinguished by their color (*L. chagosensis* is very bright yellow, small *P. heteroraphis* tend to be darker). In most cases, especially for specimens not observed in situ (i.e. dried and preserved specimens), a taxonomic decision is only possible from examination of spicule morphology, where only *P. heteroraphis* possesses the species-characteristic tripod-like small triactines. *Pericharax heteroraphis*, one of the so-called 'circum-Pacific' species, is the current target of studies on population genetics and intra-specific variation in Calcarea throughout the GBR and Coral Sea. This study will investigate whether 'widely distributed' Indo-Pacific species represent genetically distinct, reproductively isolated populations of morphologically closely related taxa ('morphospecies'), or are truly 'widely distributed' with regional populations in genetic contact (Wörheide, in preparation).

## RESULTS OF STABLE ISOTOPE ANALYSIS OF CALCAREOUS SPICULES

Bulk samples of calcareous spicules from five species of Calcinea, described in this work, and four species of Calcaronea, to be described in the second part of this series (Wörheide, in preparation), were analysed for their stable isotope values ($\delta^{13}C$, $\delta^{18}O$). These results are presented in Figure 10. Data show that Calcinea have negative $\delta^{13}C$ values and Calcaronea have positive $\delta^{13}C$ values. $\delta^{18}O$ values range from -0.28 to -1.41 in Calcaronea, and -1.39 to -2.39 in Calcinea .



**Calcaronea:**
72 *Leucandra* n.sp.
70 *Grantiopsis cylindrica*
82 *Sycon gelatinosum*
85 *Sycettusa simplex*

**Calcinea:**
80 *Clathrina helveola* n.sp.
76 *Leucaltis clathria*
84 *Clathrina luteoculcitella* n.sp.
61 *Soleniscus radovani* n.sp.
62 *Leucetta villosa* n.sp.

FIG. 10. Stable Isotope values ($\delta^{13}C/\delta^{18}O$) of calcareous spicules of nine Calcarea from Heron Island and Wistari Reef (Capricorn/Bunker Group, GBR).

## DISCUSSION

STABLE ISOTOPES. Reitner (1992) first showed that stable isotope values of calcareous spicules ($\delta^{13}C$, $\delta^{18}O$) were useful to differentiate between Calcinea and Calcaronea, which is clearly confirmed by present results. Distinct $\delta^{13}C$ values indicate that different biocalcification processes occur in each subclass, involving different fractionation processes. This is most likely a result of different cellular and/or subcellular mechanisms involved in spicule formation occurring in each subclass, as proposed by Reitner (1992), although no specific mechanisms have yet been considered. Of relevance here is the fact that the most highly developed species (i.e. with most developed canal system), *Leucandra* sp. (no. 72 in Fig. 10) and *Leucetta villosa* (no. 62 in Fig. 10), show the highest and lowest $\delta^{13}C$ values, respectively. Conversely, differences in $\delta^{18}O$ values cannot be explained at the present stage without further investigation. Further stable isotope analyses of calcareous spicules are in progress, investigating the potential value of isotopic data to support differentiation between Calcarea at the subclass, and possibly also lower taxonomic level. Since the work of Ledger (1976) and Ledger & Jones (1977) the biogenesis of calcarean spicule development was thought to be uniform throughout Calcarea, although previous data was only comprehensive for Calcaronea (*Sycon ciliatum*, *Leucosolenia complicata*; see review in Simpson, 1984). Although preliminary, present data strongly indicate the biological basis for differentiating Calcinea and Calcaronea, supporting Borojevic's et al. (1990, in press) proposal based on morphological data. However, our data also emphasise that a comprehensive and detailed re-examination of biocalcification processes is required for Calcarea in general (currently in progress), involving investigations at the cellular (SEM/TEM) and subcellular level (analysis of biogeochemistry: biomarkers, intracrystalline organic matrix; molecular techniques) (Wörheide, in prep.).

TAXONOMY. The present study describes 14 species of calcarean Calcinea,including 8 new species, whereas prior to this work only 4 species had been described for the entire GBR (Hooper & Wiedenmeyer, 1994). We have demonstrated in this preliminary study that the vast world heritage reef system of the GBR is virtually unexplored with regard to calcarean biodiversity. This is perhaps not surprising given that this study is the first comprehensive taxonomic investigation of Calcarea in Australasia in more than 50 years. We have also shown that in two genera, where only few 'classical' morphological characters can be used effectively for species identification, clear differentiation of species is very difficult, reinforcing the problems encountered by previous authors studying Calcarea, and explaining why calcarean systematics is still in flux. Biochemical and molecular studies have shown that very small morphological differences in several species of Calcarea (e.g. Atlantic *Clathrina*) correspond to quite large genetic differences, otherwise undetectable in their 'classical' morphology (Solé-Cava et al., 1991; Klautau et al., 1994). 'Classical' taxonomy thus appears to be in many cases overconservative. Characters used to differentiate species and higher taxa of Calcarea, clearly, require rethinking, making 'integrative taxonomic' approaches essential. 'Integrative taxonomy' combines different multidisciplinary approaches, which in Calcarea would involve examination of soft part ultra-structure, stable isotope and trace element analysis of spicules, molecular techniques, biogeochemical characterisation, and re-evaluation of the importance of certain 'traditional' morphological characters based on the above data.

However, a taxonomy based on, or supported by non-morphological features (e.g. molecular data) should in some way be related back to 'classical' morphology in order to be usable and practical, and this still remains a major challenge for Calcarea.

A major theme during this ongoing project in studying Australasian Calcarea is the application of modern, multidisciplinary, and integrative approaches, searching for valuable new characters in particular. The first results of this approach, presented here (stable isotope values of calcarean spicules), have shown that these new data can contribute significantly to the taxonomy of this important poriferan class, with wider applications also apparent to the biology of Porifera in general.

## ACKNOWLEDGEMENTS

This study presents initial results of a postdoctoral research project of G. Wörheide, funded by the German Academic Exchange Service (DAAD; PKZ: D/98/14533), undertaken at the Marine Biology Laboratory of the Queensland Museum, Brisbane. The financial support of the DAAD is gratefully acknowledged. We are grateful to the Queensland Museum for providing laboratory facilities and consumables used to complete the present project. We are also grateful to the Queensland Pharmaceutical Research Institute, Griffith University, Brisbane, for funding collecting activities at Heron I., Lizard I. and other GBR reefs. We also thank Stephen Cook and John Kennedy (QM) as well as Sally Leys and Nelson Luzon for field support at Heron Island. G.W. is grateful to Jean Vacelet and Nicole Boury-Esnault (Marseille, France) for helpful discussions and advice on Calcarea during the *5th International Sponge Symposium, Origin & Outlook* (Brisbane, 1998), and during the post-Symposium field trip to Heron Island. Radovan Borojévic (Rio de Janeiro, Brazil) is most gratefully acknowledged for continuous discussions on calcarean taxonomy, for providing G.W. with valuable literature, and for valuable comments on the manuscript. G.W. would also like to thank Joachim Reitner (Göttingen, Germany) for continuous support and for providing an opportunity to participate in a field trip to Heron Island in June, 1998, and to Connie Wörheide for assistance in the laboratory.

The Great Barrier Reef Marine Park Authority is acknowledged for permitting the field work (Permit nos. G98/142, G98/022).

This study was made possible by a fellowship in the course of the University-Special-Program III of the Federal Republic of Germany via the DAAD [Diese Arbeit wurde mit Unterstützung eines Stipendiums im Rahmen des Hochschulsonderprogramms III von Bund und Ländern der Bundesrepublik Deutschland über den DAAD ermöglicht].

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# SALTICIDAE (ARACHNIDA: ARANEAE) OF ORIENTAL, AUSTRALIAN AND PACIFIC REGIONS, XII. *MARENGO* PECKHAM & PECKHAM 1892 FROM PAPUA NEW GUINEA

MAREK ZABKA

Zabka, M.1999 06 30: Salticidae (Arachnida: Araneae) of Oriental, Australian and Pacific Regions, XII. *Marengo* Peckham & Peckham 1892 from Papua New Guinea. *Memoirs of the Queensland Museum* **43**(2): 893-905. Brisbane. ISSN 0079-8835.

*Marengo* is newly recorded from Papua New Guinea and five new species are described (*M. courti*, *M. platnicki*, *M. proszynskii*, *M. rafalskii* and *M. variratae*). Remarks on relationships and distribution are given. ❐ *Salticidae*, *Marengo*, *taxonomy*, *new species*, *Papua New Guinea*.

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New Guinea, being very diverse in topography, floristic formations and climate, and having a complicated geological history, is one of the richest salticid speciation centres in the tropics. The zoogeographical relationships between New Guinea, SE Asia, Australia and western Pacific archipelagos have long been discussed and resulted in different conclusions, depending on taxon level, its age, dispersal power or habitat requirements (e.g. Berland, 1934; Lehtinen, 1980, 1996; Zabka, 1991b, 1993; Prószynski, 1996).

Over 50 salticid genera from New Guinea, mostly from its Papuan part, have been recorded previously (Zabka, 1993), although *Marengo*, considered here, is new for this list. Established by Peckham & Peckham (1892) for *M. crassipes*, it includes 7 oriental species, known from Sri Lanka, Malaysia, Sumatra, Java, Borneo and Philippines, and 2 ethiopian species reported from Kenya, Tanzania, Congo, Zaire, South Africa and Angola, all of them revised by Wanless (1978). Some undescribed species have also been found in Bali, Lombok, Ambon, Sulawesi, Malaysia, Krakatoa and Thailand (Deeleman & Prószynski, unpubl.; Zabka, unpubl.).

## MATERIAL AND METHODS

Specimens were collected by David J. Court, some with my own participation, in the Central Province of Papua New Guinea; all are deposited in the Queensland Museum, Australia.

Description format follows my earlier papers (e.g. Zabka, 1991a). Dissected epigynes were cleaned in lactic acid for 10-30 min. or digested in 10% KOH for 12-48 hr at room temperature, rinsed in distilled water, stained in ethanol solution of chlorazol black E under control and mounted in glycerine. Drawings were made using a grid system and Nikon microscopes.

Abbreviations: AEW = anterior eyes width, AL = abdomen length, CL = cephalothorax length, EFL = eye field length, PEW = posterior eyes width.

## **Marengo** Peckham & Peckham, 1892

*Marengo* Peckham & Peckham, 1892: 66; Simon, 1901: 492; Bonnet, 1957: 2714; Wanless, 1978: 259; Brignoli, 1983: 627; Prószyński, 1971: 427, 1990: 203; Platnick, 1993: 776, 1997: 901.

TYPE SPECIES. *Marengo crassipes* Peckham & Peckham, 1892, by monotypy.

DIAGNOSIS (for Papua New Guinean species). *Marengo* differs from other ant-like salticid genera by the following characters: carapace flat, surface papillate; abdomen dark with transverse light pigmented band; first legs massive, tibiae swollen, with 2 rows of strong, dagger-like ventral spines and with dense fringe; embolus twisted, set retrolaterally at the top of tegulum, not around it; epigyne poorly sclerotised; copulatory openings indistinct, insemination ducts long.

DESCRIPTION. Ant-mimicking spiders. Body 2.5-5mm long. Carapace elongate and slender, rather flat, surface distinctly textured, papillate, fovea lacking. Eye field with 2 darker spots, occupies ≈40% of carapace length. Eyes in 3 rows, though anterior laterals are set above and behind medians. Posterior median eyes midway between anterior and posterior laterals. Abdomen elongate, with transverse light band, sometimes

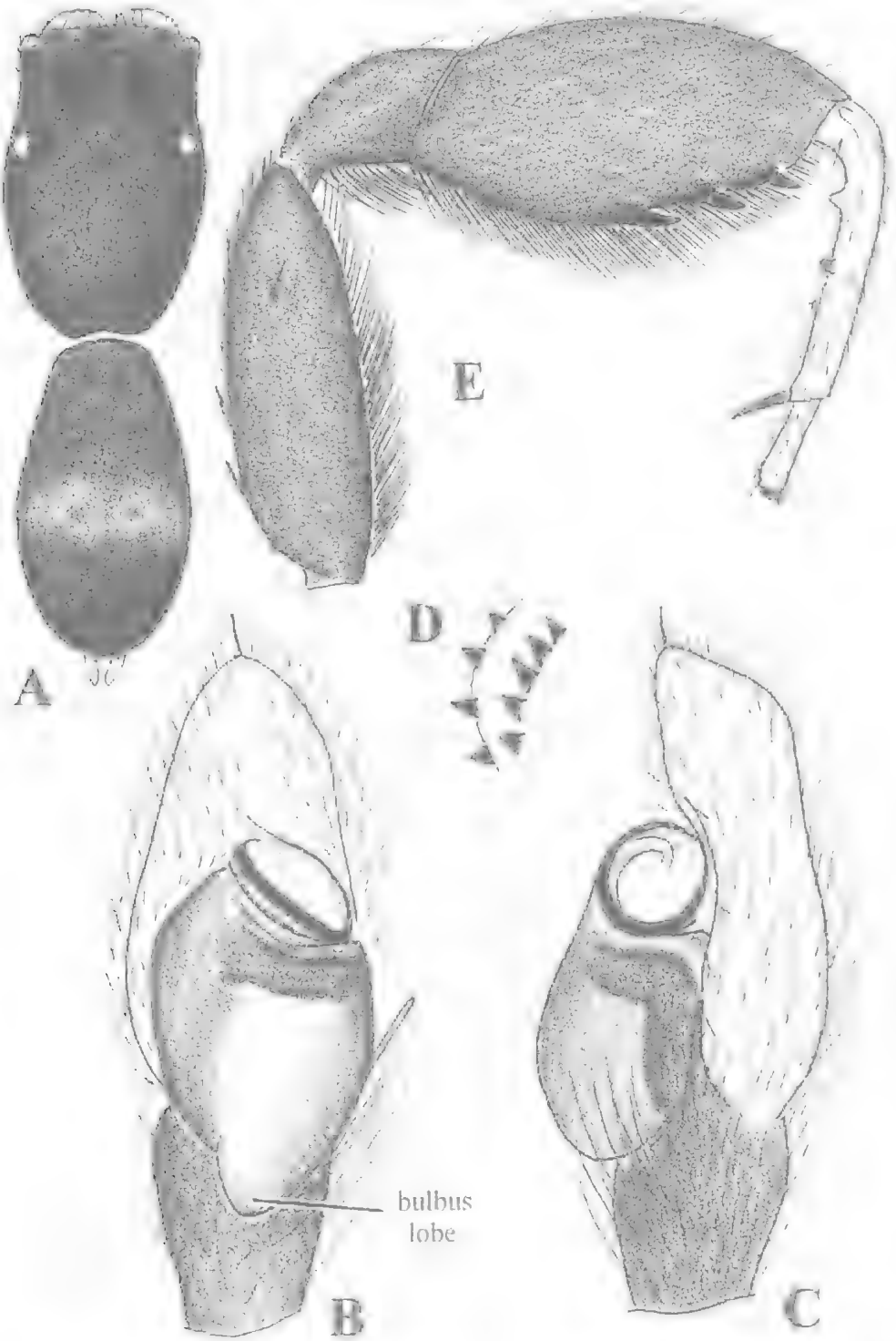



FIG. 1. *Marengo courti* sp. nov. holotype QMS42506, male. A, general appearance; B, C, palpal organ; D, cheliceral dentition; E, leg 1

covered with white hairs. Male abdomen shiny and with weakly marked scutum. Clypeus narrow, backwards sloping. Cheliceral teeth showing pluridentate pattern. Promargin with 3-6 and retromargin with 5-6 separate teeth, showing individual variation. Maxillae, labium and sternum elongate, the latter scutiform. First legs long, much heavier than others, held in mantis-like manner, their tibiae swollen and with ventral fringe of dense stiff hairs. In males anterior legs longer but less massive, additionally their femora and patellae fringed. Ventral tibial spines massive, dagger-like, in prolateral and retrolateral rows, of 3 (in one case, 4), sometimes differing in number in the same specimen. Metatarsal spines, especially proximal ones, reduced in size to small spurs. Metatarsi in males with proximal ventral knob. Other legs slender. Leg formula: I-IV-II-III. Male palpal organ very uniform in structure, showing little variation between species. Cymbium with apical bristle, bulbus bag-like, sometimes with distinctive posterior lobe. Spermophore more or less translucent, meandering in its median part (if visible). Embolus long, coiled distally around membranous haematodocha. Tibial apophysis slender. Epigyne weakly sclerotised, in the form of 2 delicate depressions divided by median ridge. Copulatory openings indistinct, leading to wide insemination ducts becoming narrower and more sclerotised before entering the thick-walled, small spermathecae. Insemination ducts with or without accessory glands.

AFFINITIES. Wanless (1978) and Platnick (1984) hypothesise relationships between *Marengo*, oriental *Mantisatta* and american *Cheliferoides*. Indeed, the genera share similarities in genitalic pattern and leg morphology, the latter character an adaptation to hunting strategy rather than the result of relationships. *Cheliferoides* is known to be a crevice (bark) dweller with 1st legs heavier than others. *Mantisatta* lives in termite nests, hunting in a mantis-like manner (Cutler & Wanless, 1973). There is no information on crevice dwelling in *Marengo*. Some species are rainforest foliage inhabitants, others may be found in mangroves. It is likely that, as in some other salticid genera (e.g. *Diolenius*), *Marengo* specimens may mimic flies in reverse, with first legs held in the manner of flies' wings.

Three Australian genera, *Rhombonotus*, *Damoetas* and *Ligonipes*, resemble *Marengo* in habitus and leg structure (Davies & Zabka, 1989) but the genitalia show they are not closely related.

The presence of 4 eye rows, the character mentioned by Wanless (1978), also is of limited value. Unlike the Spartaeinae, Lyssomaninae or *Athamas*, the posterior lateral eyes in *Marengo* do not form a distinctive 4th row and their position cannot be considered as important phylogenetically.

**Marengo courti** sp. nov.
(Figs 1A-E, 2A-E)

ETYMOLOGY. For David J. Court (Boroko, Papua New Guinea, now Singapore), arachnologist and the collector of specimens studied in this paper.

MATERIAL. HOLOTYPE: QMS42506, M, PNG, Central Province, Brown R., lowland rainforest, 16.vii.1988, D.J. Court, M. Zabka. ALLOTYPE: QMS42507, F, same data. PARATYPES: QMS42508, 3 F's, same data.

DIAGNOSIS. Bulbus with distinctive lobe, tibial apophysis shorter than in the next species. Epigyne with extended membranous pseudopocket (Fig. 2B, arrow). Insemination ducts without accessory glands.

*Male* (Fig. 1A). CL 1.87, EFL 0.80, AEW 1.19, PEW 1.27, AL 2.08. Carapace brown, without numerous white hairs, eye field with 2 darker spots, eye surrounding black. Abdomen grey, transverse band slightly lighter. Spinnerets whitish. Clypeus, chelicerae, maxillae and labium greyish-brown, the latter with lighter tips. Cheliceral promargin and retromargin with 4 and 5 teeth, respectively (Fig. 1D). Sternum orange, venter grey. Leg I (Fig. 1E): femur, patella and tibia brown, laterally darker, ventrally with dense hairs, femur also with dorsal hairs. Legs II and III yellowish with brown sides of femur. Leg IV with darker sides of femur, patella, tibia and metatarsus. Palpal as illustrated in Fig. 1B,C.

*Female* (Fig. 2A). CL 1.71, EFL 0.72, AEW 1.14, PEW 1.14, AL 2.23. Clypeus brown. Chelicerae, maxillae, labium and sternum dirty-orange, the first with 3 promarginal and 6 retromarginal teeth (Fig. 2E). Leg I (Fig. 2D): femur and tibia with greyish-brown sides, the latter with ventral fringe, patella distally darker. Leg II: sides of femur with dark distal spots, patella, tibia and metatarsus greyish, especially retrolaterally. Leg III: retrolateral femur with grey distal spot, retrolateral patella, tibia and metatarsus with grey bands. Leg IV: femur sides grey, patella, tibia and metatarsus with retrolateral bands. Epigyne and

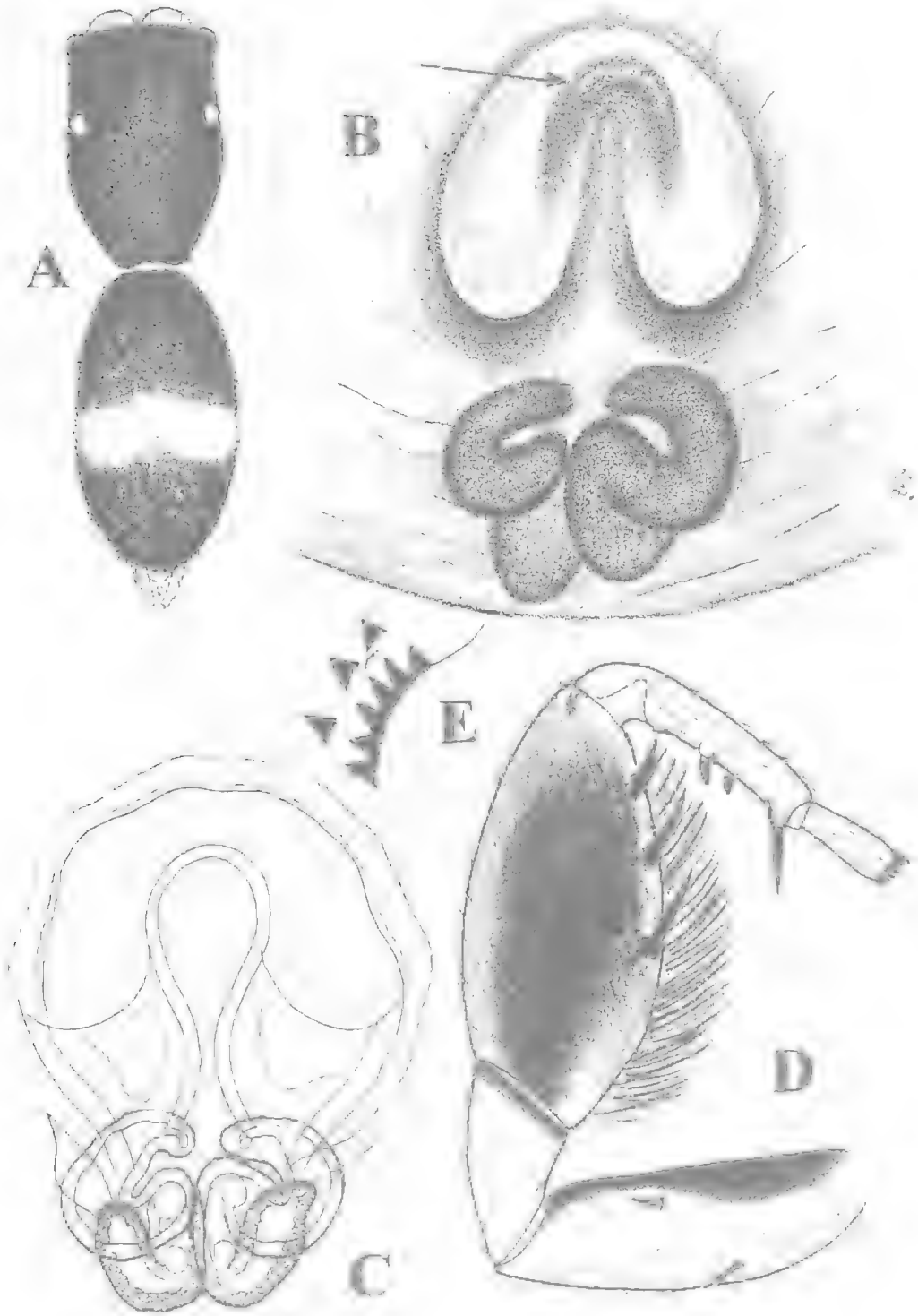



FIG. 2. *Marengo courti* sp. nov. allotype QMS42507, female. A, general appearance; B, C, epigyne and internal genitalia; D, leg I; E, cheliceral dentition.

internal genitalia as shown in Fig. 2B,C. Other characters as in male.

**Marengo platnicki** sp. nov.
(Figs 3A-E, 4A-E)

ETYMOLOGY. For Dr Norman I. Platnick (American Museum of Natural History, New York).

MATERIAL. HOLOTYPE: QMS42509, M, PNG, Central Province, SW side of main Astrolabe Ra., adjacent Sirinumu Dam, 15.VII.1986, D.J. Court. ALLOTYPE: QMS42510, F, same data.

DIAGNOSIS. Male carapace sides with white hairs. Palpal tibial apophysis laterally bent and longer than in the previous species, bulbus with posterior lobe. Female insemination ducts proximally very wide, with distinctive accessory glands.

*Male* (Fig. 3A). CL 1.92; EFL 0.78; AEW 1.19; PEW 1.19; AL 2.23. Carapace brown, sides with white hairs. Abdomen grey, glittering, laterally darker, with light transverse band. Clypeus and frontal chelicerae brown, the latter with 4 promarginal and 6 retromarginal teeth (Fig. 3E). Sternum orange, venter grey. Leg I (Fig. 3D): femur, patella and tibia brown with ventral fringe, dorsal parts of femur lighter with distal hairs, metatarsus and tarsus yellow. Other legs yellowish, II and III with darker sides, IV with darker posterior sides of femur, patella and tibia. Palpal organ as illustrated in Fig. 3B, C.

*Female* (Fig. 4A). CL 1.82; EFL 0.72; AEW 1.09; PEW 1.14; AL 2.21. Generally coloured as male, behind the eye field distinctive white hairs. Clypeus brown. Chelicerae dirty-light-brown, with 4 promarginal and 5 retromarginal teeth (Fig. 4D). Maxillae and labium dirty orange with lighter tips. Sternum dirty-yellow, venter beige. Leg I (Fig. 4E): lateral femur and tibia brown-grey, the latter with ventral fringe. Leg II: retrolateral femur, patella and tibia with dark band. Leg IV: distal femur laterally dark, retrolateral tibia and metatarsus with dark band. Epigyne and internal genitalia as illustrated in Fig. 4B,C.

**Marengo proszynskii** sp. nov.
(Fig. 5A-H)

ETYMOLOGY. For Prof. Jerzy Prószyński, prominent Polish specialist in taxonomy and biogeography of Salticidae.

MATERIAL. HOLOTYPE: QMS42511, M, PNG, Central Province, Brown R., lowland rainforest, 13.VII.1988, M. Zabka. ALLOTYPE: QMS42512, F, same data.

DIAGNOSIS. Male abdomen with 2 light spots rather than transverse band. Tibial apophysis bent aside, posterior bulbus' lobe not distinctive, embolus rather massive. Female internal genitalia multi-chambered, insemination ducts proximally widened, accessory glands not visible.

*Male* (Fig. 5A). CL 2.13, EFL 0.88, AEW 1.30, PEW 1.35, AL 2.34. White hairs on carapace rather scanty. Abdominal scutum poorly marked, sides with characteristic light spots and narrow stripes. Clypeus brown. Chelicerae orange brown, with 4 promarginal and 6 retromarginal teeth (Fig. 5D). Maxillae and labium dirty brown with lighter tips. Sternum pale-orange, venter grey. Leg I: femur dirty-brown with ventral and dorsal fringe, the first being less distinctive; patella and tibia lighter, especially their dorsal and ventral surfaces, both with ventral fringes; metatarsus and tarsus yellowish. Leg II: sides of femur dark-grey. Leg III: retrolateral side of femur grey. Leg IV: sides of femur, retrolateral tibia and metatarsus grey. Other parts of legs yellowish. Palpal organ as illustrated in Fig. 5B,C.

*Female* (Fig. 5E). CL 1.61, EFL 0.67, AEW 0.90, PEW 1.01, AL 2.02. Behind PLE distinctive white hairs. Clypeus brown. Chelicerae dirty-orange, with 3 promarginal and 5 retromarginal teeth (Fig. 5H). Maxillae greyish-orange, labium darker, sternum orange with darker margin. Venter centrally light-grey, towards sides darker. Leg I: sides of femur and tibia dark-grey, the rest yellowish, tibia with ventral fringe. Leg II: prolateral tibia and retrolateral femur, patella and tibia with grey band. Leg III: retrolateral femur with distal grey spot. Leg IV: distal sides of femur, retrolateral tibia and metatarsus grey. Other parts of podomeres II-IV yellowish. Epigyne and internal genitalia as shown in Fig. 5F,G. Other characters as in male.

**Marengo rafalskii** sp. nov.
(Fig. 6A-D)

ETYMOLOGY. For Prof. Jan Rafalski (1909-1995), prominent Polish arachnologist.

MATERIAL. HOLOTYPE: QMS42513, M, PNG, Central Province, Brown R., lowland rainforest, 29.VI.1988, D.J. Court. PARATYPE: QMS42514, M: same locality, from foliage, 13.VII.1988, M. Zabka.

DIAGNOSIS. Eye field covered with dense white hairs. Bulbus elongate, with posterior lobe.

*Male* (Fig. 6A). CL 1.97, EFL 0.83, AEW 1.11, PEW 1.19, AL 2.23. Carapace brown, distinctive

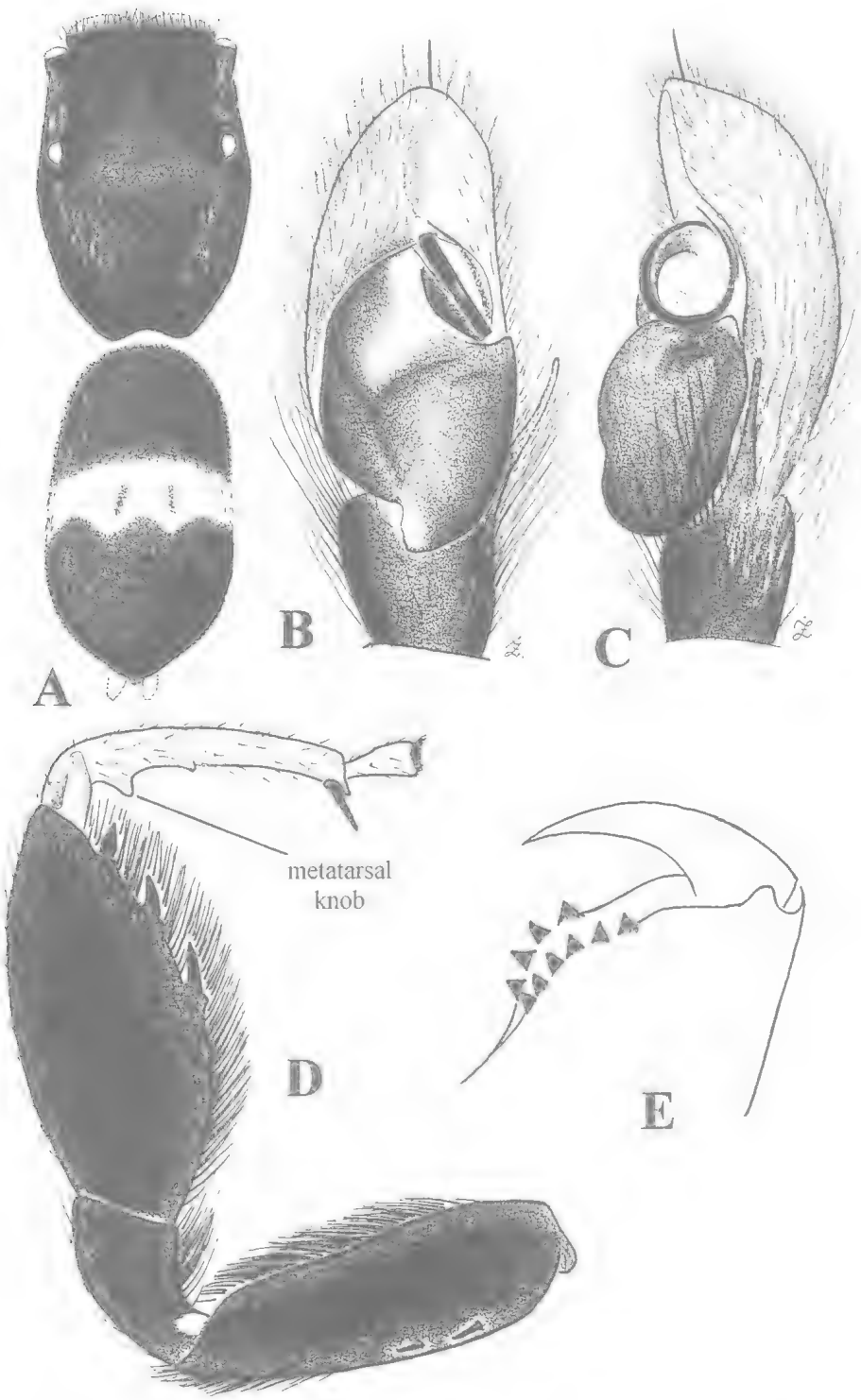



FIG. 3. *Marengo platnicki* sp. nov. holotype QMS42509, male . A, general appearance; B, C, palpal organ; D, leg I; E, cheliceral dentition.

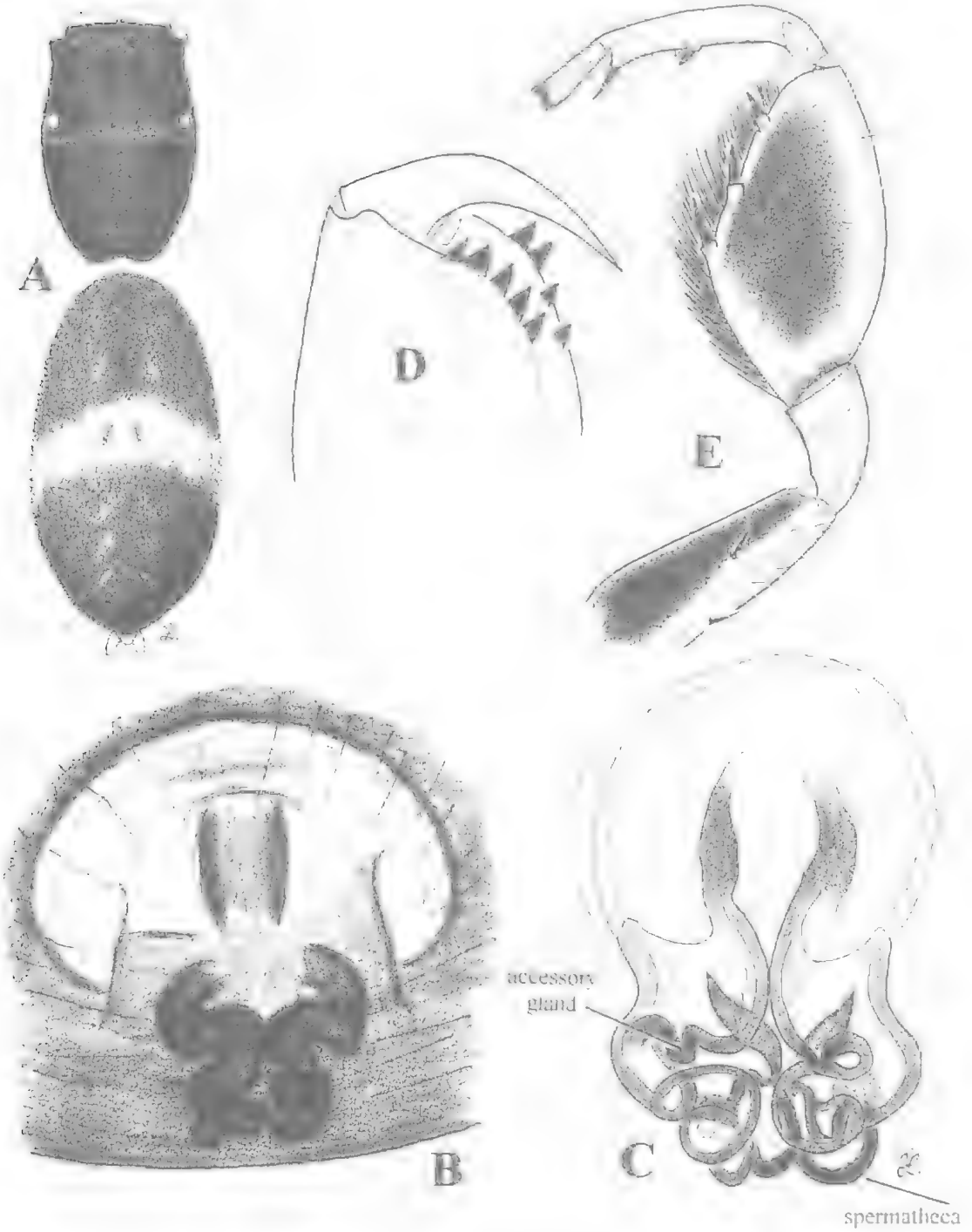



FIG. 4. *Marengo platnicki* sp. nov. allotype QMS42510, female. A, general appearance; B, C, epigyne and internal genitalia; D, cheliceral dentition; E, leg I.

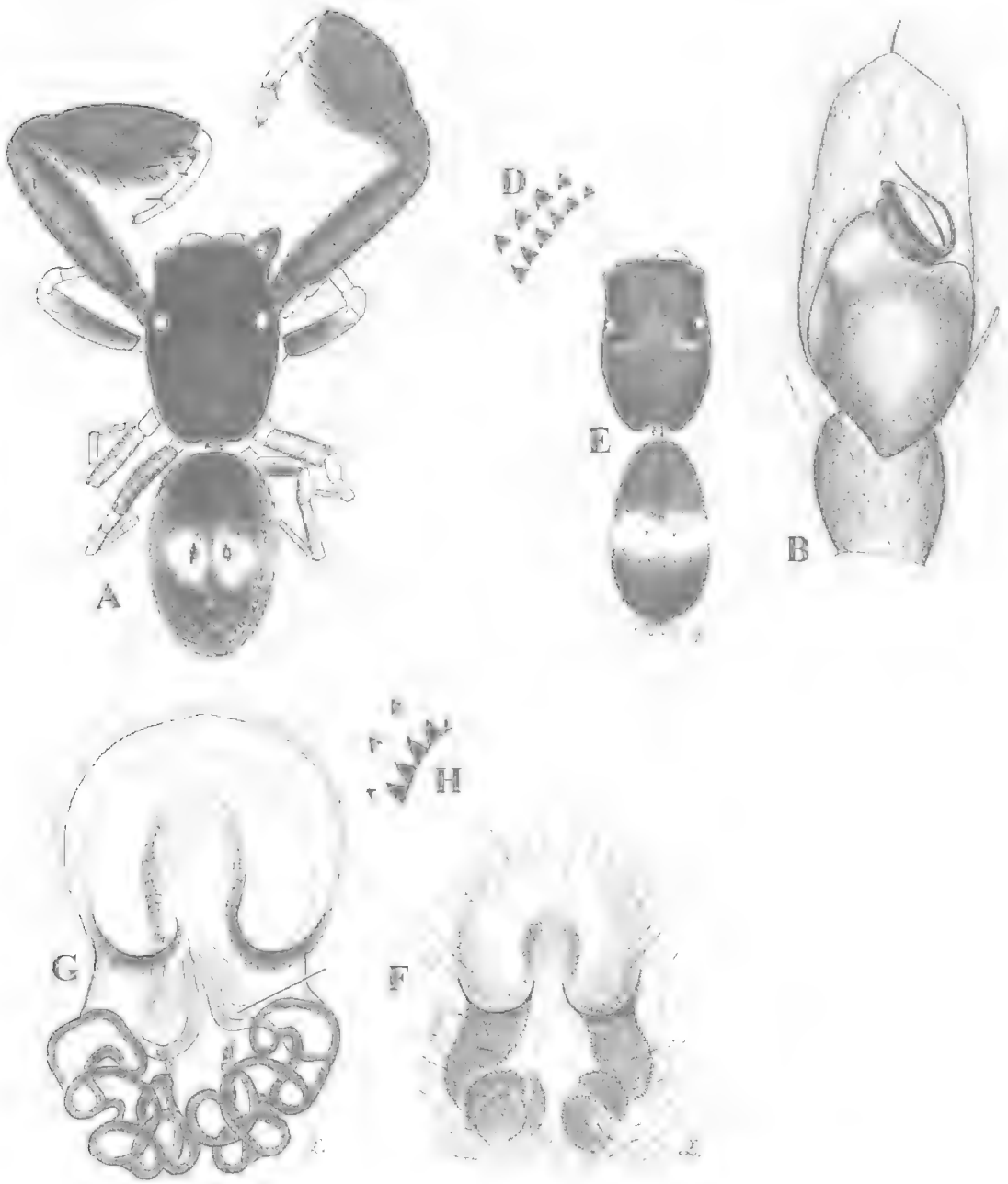



FIG. 5. *Marengo proszynskii* sp. nov. A-E, holotype QMS42511, male; A, general appearance; B, C, palpal organ; D, male cheliceral dentition; E-H, allotype, QMS42512, female; E, general appearance; F, G, epigyne and internal genitalia; H, cheliceral dentition.

light hairs extending behind PLE. Eye surroundings darker. Abdomen dark-grey with light transverse band and 2 darker apodemes. Spinnerets whitish. Clypeus brown, chelicerae lighter, with 5 prolateral and 6 retrolateral teeth (Fig. 6D). Pedipalps' proximal podomeres grey-brown, distal gradually lighter to whitish. Maxillae and labium dirty-orange, sternum lighter.

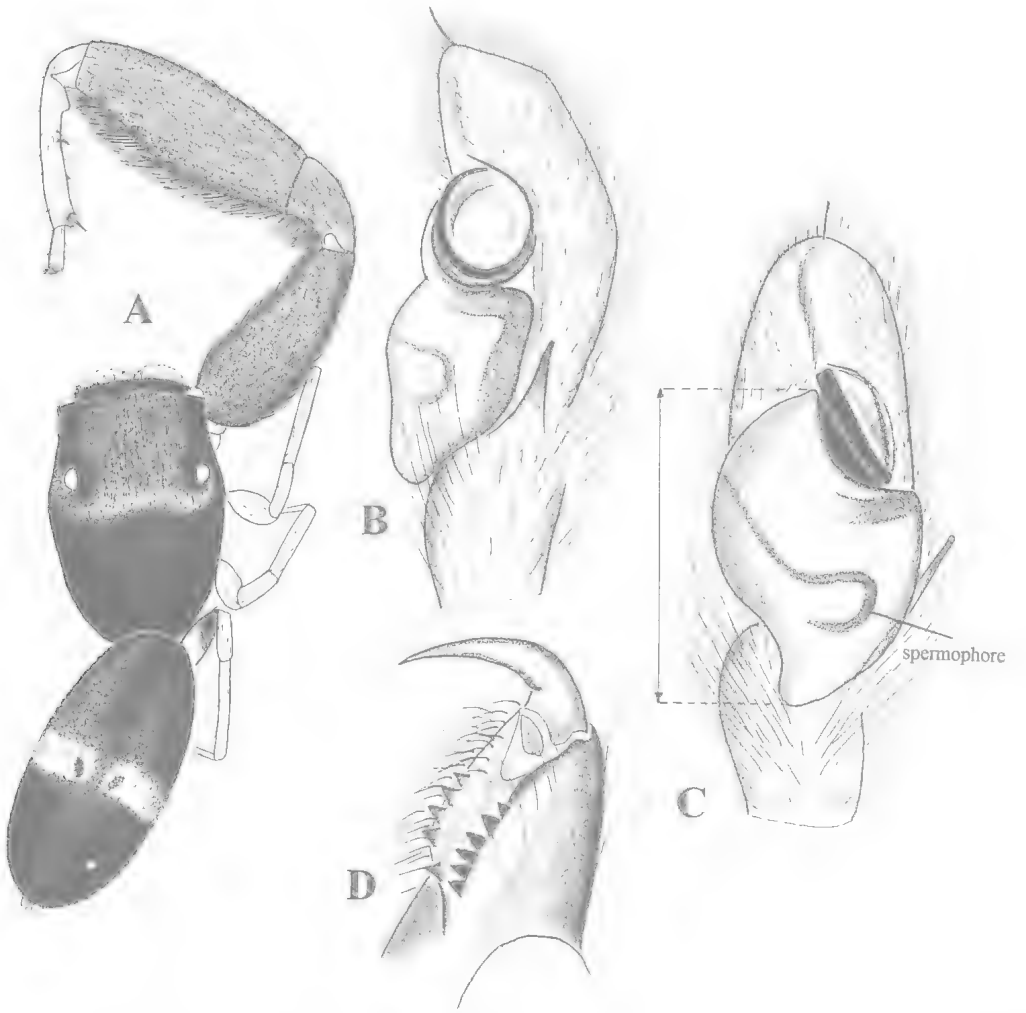



FIG. 6. *Marengo rafalskii* sp. nov. holotype, QMS42513, male. A, general appearance; B, C, palpal organ; D, cheliceral dentition.

Venter grey, centrally lighter. Leg I: massive and long, femur, patella and tibia greyish-brown, dorso-ventrally lighter, all with ventral fringes. Leg II: femur with lateral grey bands. Leg III: retrolateral side of femur grey. Leg IV: sides of femur grey, along retrolateral surface of patella, tibia and metatarsus grey band. Other podomeres of all legs white-yellow. Palpal organ as in Fig. 6B,C.

**Marengo variratae** sp. nov.
(Figs 7A-E, 8A-E, 9A-F)

ETYMOLOGY. For the type locality.

MATERIAL. HOLOTYPE: QMS42515, PNG, Central Province, Varirata National Park, 2.VI.1985, D.J. Court. ALLOTYPE: QMS42516, F, same data. PARATYPES: QMS42517-42518, 2 F's, same locality, 23.VI.1985, 24.VIII. 1985, D.J. Court, M, 2 juv., Central Province, Brown R., lowland rainforest, 29.VI.1988, D.J. Court.

DIAGNOSIS. Male carapace without numerous white hairs. Bulbus short, posterior lobe small. Female insemination ducts anteriorly narrow, with distinctive accessory glands.

*Male* (Fig. 7A). CL 2.23, EFL 0.93, AEW 1.45, PEW 1.50, AL 2.65. Carapace brown, eye surrounding black. Abdomen grey with light transverse band. Spinnerets whitish. Clypeus brown, chelicerae lighter with 4 prolateral and 5

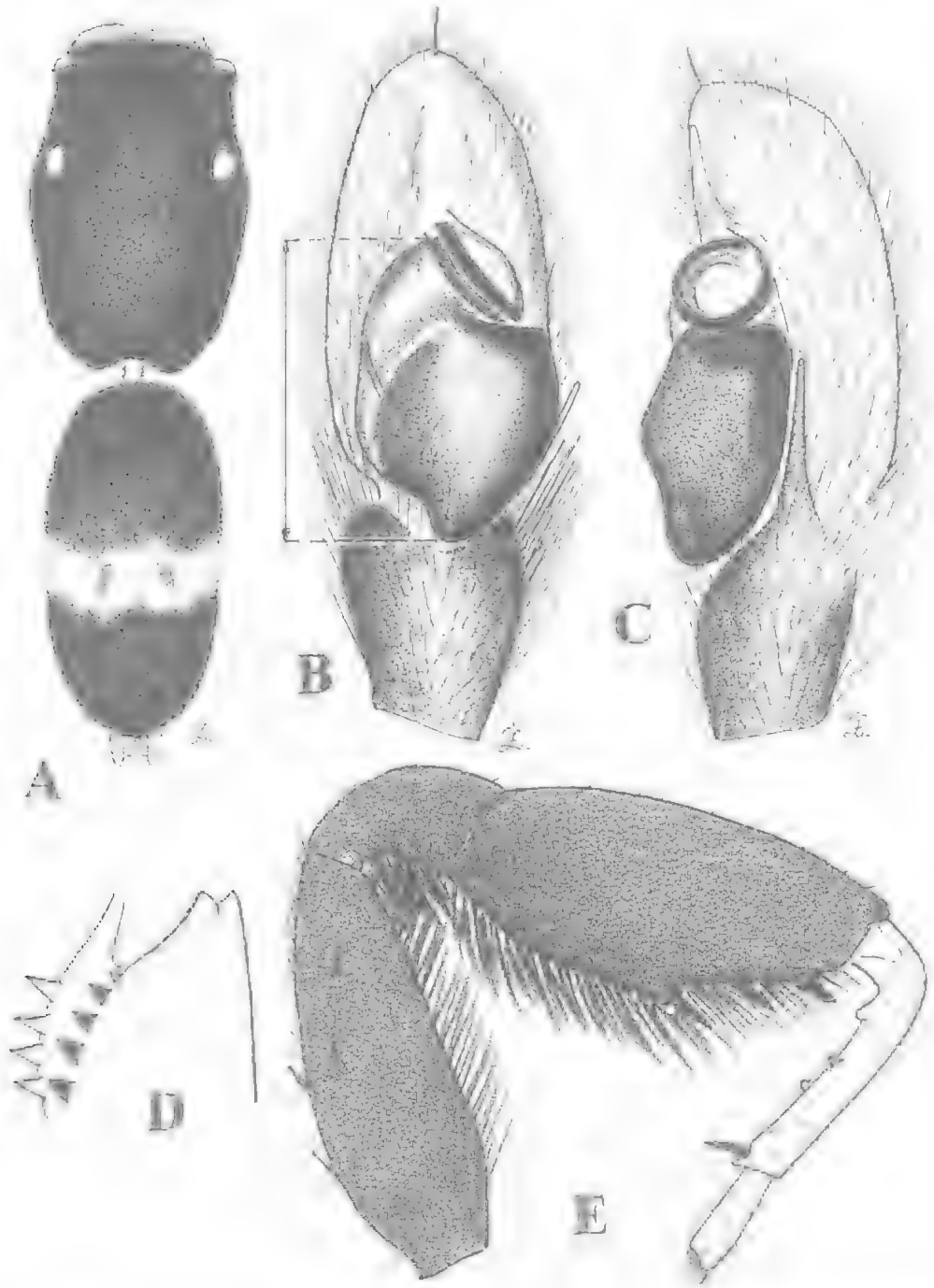



FIG. 7. *Marengo variratae* sp. nov. holotype, QMS42515, male. A, general appearance; B, C, palpal organ; D, cheliceral dentition; E, leg I.

retrolateral teeth. Maxillae and labium grey-brown with lighter tips. Sternum orange, venter grey. Leg I (Fig. 7E): femur, patella and tibia dirty-light-brown, lighter dorso-laterally, each

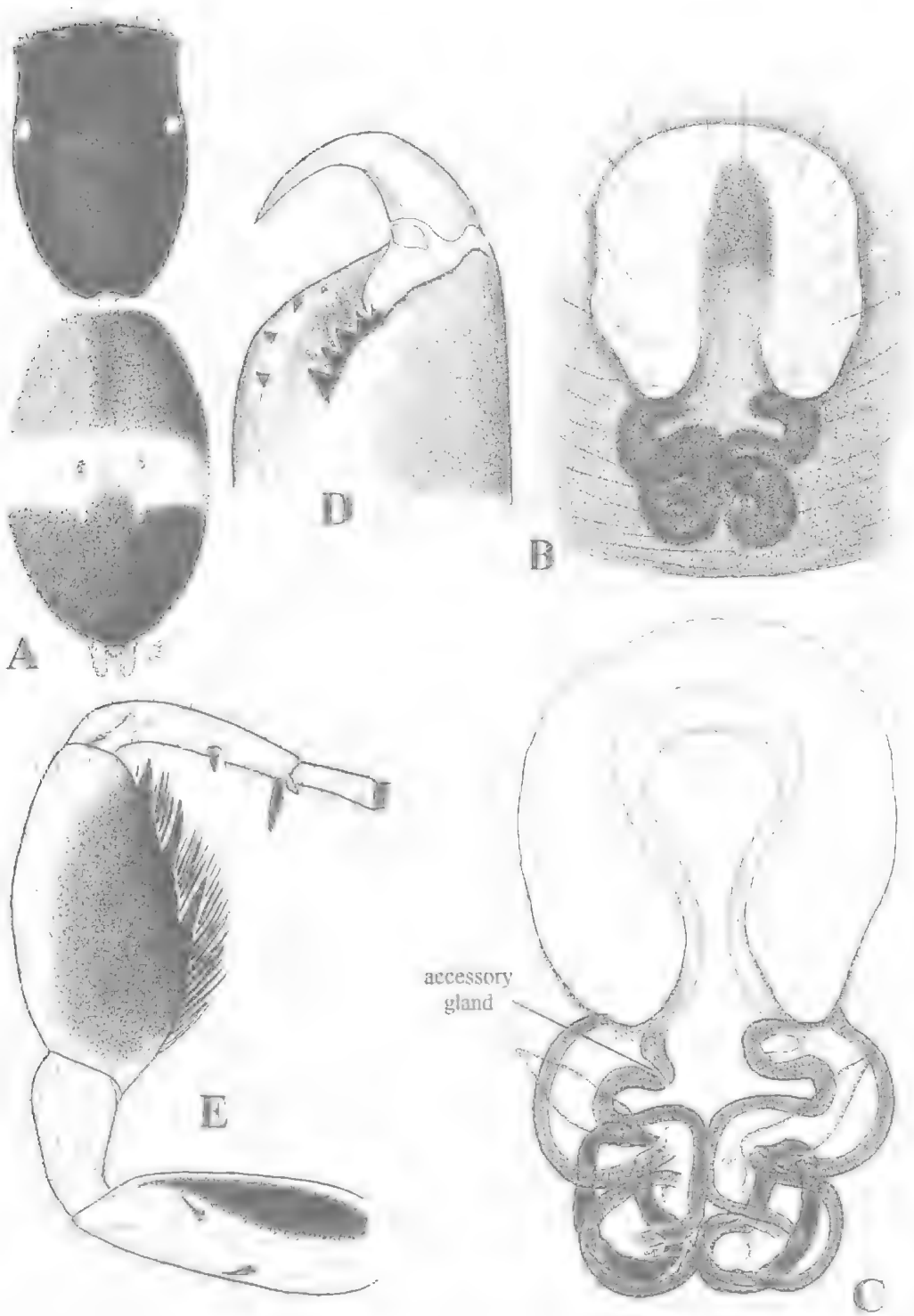



FIG. 8. *Marengo variratae* sp. nov. A-D, paratype, QMS42517, female. A, general appearance; B, C, epigyne and internal genitalia; D, cheliceral dentition. E, allotype, QMS42516, female, leg 1.

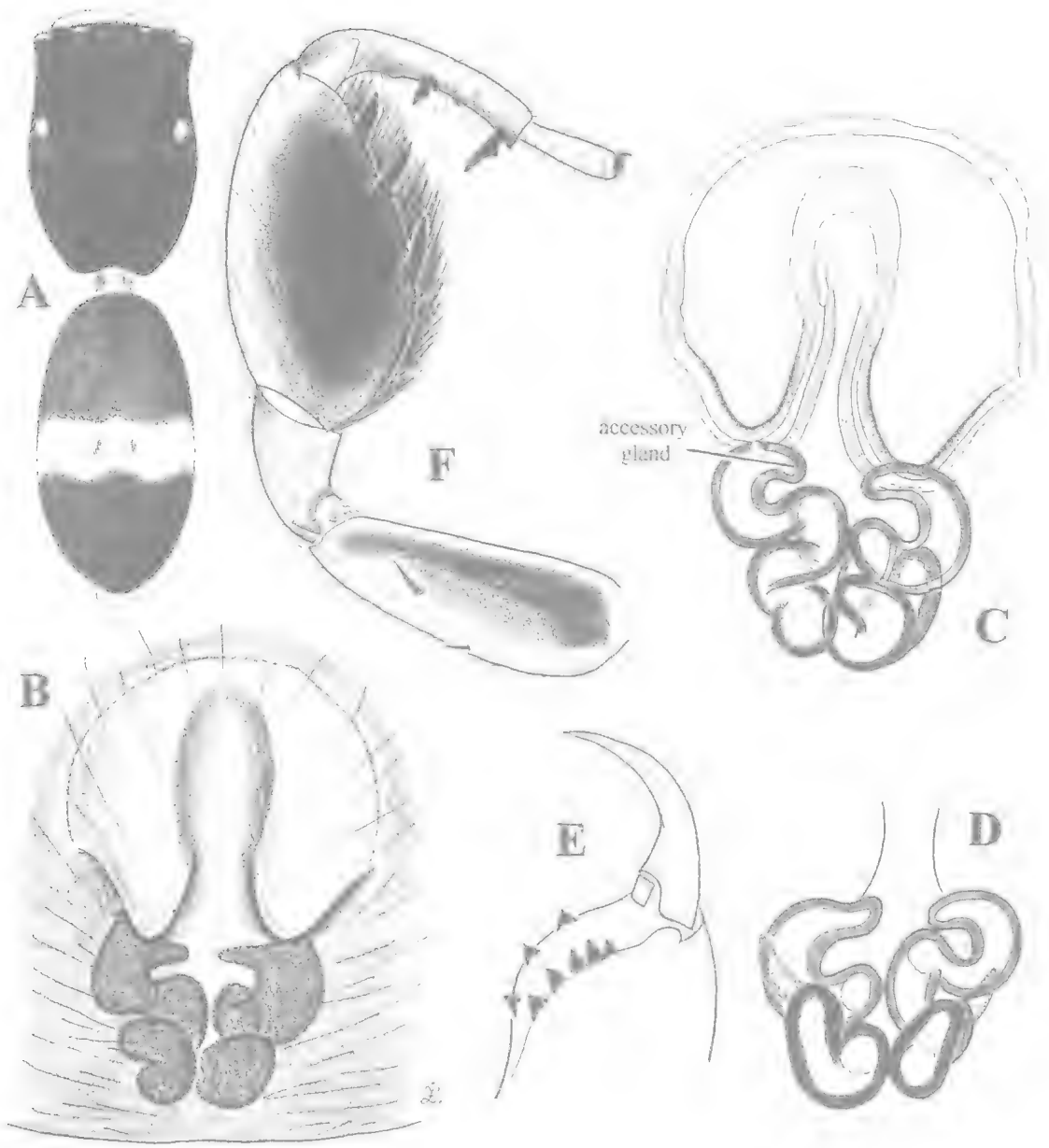



FIG. 9. *Marengo variratae* sp. nov. paratype, QMS42518, female. A, general appearance; B-D, epigyne and internal genitalia; E, cheliceral dentition; F, leg I.

with ventral fringe, femur also with dorsal hairs; metatarsus and tarsus yellow. Leg II-IV: femur laterally grey, the rest whitish-yellow. Palpal organ as illustrated in Fig. 7B,C.

*Female* (Figs 8A, 9A). CL 1.76, EFL 0.78, AEW 0.98, PEW 1.14, AL 2.54. Behind PLE scattered white hairs. Chelicerae yellow-orange, with 3-4 prolateral and 5 retrolateral teeth. Maxillae and labium light-orange with lighter tips. Venter with large light path being extension of the dorsal belt. Leg I (Figs 8E, 9F): lateral sides of femur and tibia grey-brown, other podomeres whitish; tibia

swollen with ventral scopula. Legs II and III whitish. Leg IV: sides of femur and retrolateral tibia with grey band. Other podomeres whitish. Epigyne as illustrated in Figs 8B,C & 9B-D. Other characters as in male.

## ACKNOWLEDGEMENTS

The research was partly conducted under receipt of an Australian Museum Fellowship. M. Gray (Australian Museum, Sydney), V. Davies, R. Raven (Queensland Museum, Brisbane) and J. Waldock (Western Australian Museum, Perth) were most gracious and cooperative during my stay in their departments. D.J. Court (Boroko, now Singapore) is acknowledged for his generous hospitality and highly professional help while visiting Papua New Guinea. I am especially indebted to V.T. Davies (Queensland Museum, Brisbane) and M. Harvey (Western Australian Museum, Perth) for useful comments on the typescript and to C. Deeleman (Ossendrecht) for providing comparative specimens from Indonesia. The research was supported by Komitet Badan Naukowych (Projects 18/91/S and 512/93/W).

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